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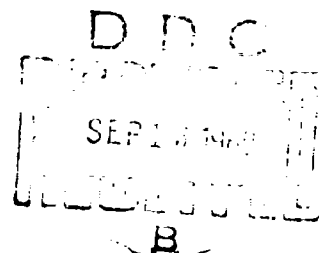
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84

INVESTIGATIONS ON GERMINATION OF UREDOSPORES
OF STRIPE RUST

(Puccinia striiformis West.)

Dissertation
approved by the Faculty of Natural Science
and Philosophy of the Carolo-Wilhelmina
Technical Academy at Braunschweig for
Attainment of the Degree of Doctor of
Natural Science (Dr.rer.nat.)

by

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Submitted: 9 March 1964
Oral Examination: 15 April 1964
Reporter: Professor Dr. K. Hassebrauk
Associate Reporter: Professor Dr. W. H. Fuchs

1964

TABLE OF CONTENTS

	<u>Page</u>
I. INTRODUCTION.....	1
II. MATERIAL AND METHODS.....	2
III. EXPERIMENTAL PART.....	4
A. Morphological Investigations.....	4
1. Size of Uredospores.....	4
2. The Growth Pattern of Germ Tubes.....	8
3. The Formation of Vesicles and Secondary Hyphae.....	13
B. Germination Physiological Investigations.....	18
1.a) The effect of various agar types and concentrations on germination.....	19
1.b) The effect of different gelatin sub- strates on germination.....	24
1.c) Effect of hydrogen ion concentrations on germination.....	26
2. The Effect of Outside Factors during the Formation of Spores on the Subsequent Germination Reaction.....	31
2.a) Host plant.....	32
2.b) Temperature.....	32
2.c) Humidity of air.....	34
2.d) Light.....	35
3. The Direct Effect of Environmental Conditions on Germination.....	36

TABLE OF CONTENTS (continued)

	<u>Page</u>
3.a) Light.....	36
3.b) Temperature.....	38
B. 4. The Fructification Period as a Characteristic Feature of Individual Stripe Rust Races.....	44
B. 5. Investigations on the Self-Inhibition of Germinating Stripe Rust Uredospores.....	45
5.a) Investigations concerning the germination inhibiting effect of aqueous spore diffusates.....	47
5.b) Investigations on the nature of the inhibiting agent.....	49
B. 6. Relationship between the Development of Weather Conditions and the Germination of Uredospores.....	54
IV. DISCUSSION.....	62
V. SUMMARY.....	*
VI. BIBLIOGRAPHY.....	69
RESUMÉ.....	79

*[The summary (in German and English) is not included
in this translation.]

I. INTRODUCTION

Eriksson and Henning (1896) were the first to make a thorough investigation on the stripe rust (Puccinia striiformis West.), which resulted in a number of important observations and points of attack for further investigations.

In connection with germination tests Eriksson and Henning stated that the germination capacity of the uredospores of stripe rust is "highly erratic." Subsequently, this judgment as an erratic type of rust was found repeatedly (Schaffnit, 1909; Becker, 1928) precisely with authors who must be considered unbiased in the evaluation of germination and infection tests thanks to years of intensive work with grain rusts and particularly stripe rust (Straib, Newton and Johnson, Manners). Only Wilhelm (1931) pointed out once "that nature has probably not granted the stripe rust the right of 'erratic character' for its germination physiological reaction, but that here a certain regularity forms the basis." Wilhelm has tried for the first time to explain the seemingly contradictory findings by a particularly fine capacity of reaction of this type of rust to various environmental factors.

Indeed, subsequently, the investigations made by a few authors who studied more thoroughly the reaction of stripe rust to germination and infection have led to the recognition that Puccinia striiformis responds to various influences of the environment, among which, for instance, temperature is attributed a special significance much stronger than other types of rusts.

Therefore, under these circumstances it is evident that literature often contains data on certain properties of stripe rust which are contradictory and require clarification. In addition, other observations require a checking, confirmation and extension. These requirements are applicable particularly to investigations which concern the germination of uredospores.

After Straib (1937) had found for the first time striking differences in the germination of various physiological races, it was found necessary to examine the germination of uredospores of various partly new stripe rust races which had been isolated during the past few years, taking into account the differences between the factors of cultivation and germination. A safe knowledge of germinating requirements is one of the premises for reliable infection tests and the possibility provided thereby of establishing the physiological specialization with a satisfactory degree of certainty.

Following is a report on such investigations.

II. MATERIAL AND METHODS

The investigations were made with biotypes (clonic types) of stripe rust (Puccinia striiformis West. = P. glumarum [Schm.] Eriksson and Henning). When "races" are mentioned in the following, we mean biotypes which are assigned to a certain physiological race. The races were determined and numbered according to the method developed by E. Fuchs (1960; and unpublished). The origin of a race from a certain country has been marked by me, if applicable, by letters added in parentheses.

Legend:

D = Germany	Ke = Kenya
F = France	NL = Netherlands
GB = Great Britain	Sz = Switzerland
Gr = Greece	T = Turkey
Is = Israel	

The additional letter "A" does not indicate any special origin but states that this race leads to a high degree of affection on the supplementary wheat test variety "Lee" (according to E. Fuchs).

The races appearing on wheat were propagated on the highly sensitive wheat varieties "Michigan Amber" and Triticum dicoccum tricoctum, the races affecting barley propagated on summer barley "Fong Tien" and inoculated for control purposes from time to time through the test assortment.

The host plants were cultivated, 8 to 10 per pot, in loamy sand with the addition of some compost earth in the greenhouse at approximately 15 to 20° C. The inoculation was effected in the one-leaf stage in the usual manner by spreading a spore suspension in a 0.1 % agar solution with a cotton wool brush on

the upper side of the germination leaf. Subsequently, the infected plants remained in a special greenhouse, first for two days in an atmosphere saturated with water vapor, then standing freely; the cover was taken off only with the beginning of sporulation.

The temperature of this greenhouse was kept by appropriate devices (cooling units, heating) independent of the outside temperature, at 15° C (±2°). During the winter half year the test plants were exposed to extra light (fluorescent tubes of Osram de Luxe and Sylvania White de Luxe).

For special experiments an air-conditioned room with a constant temperature of 15° C (±1°) was made available temporarily, having an exclusive artificial source of light (Sylvania White de Luxe, light intensity 3500 to 4000 Lux at the level of the experimental plants, with an illumination of 12 hours daily). The relative humidity of the air was in line with average greenhouse conditions.

The races used within a test series were always propagated at the same time under the same environmental conditions. The spores formed immediately after start of sporulation were first removed, and only the uredospores newly formed during 24 to 48 hours were taken off in order to obtain material of the same age for the comparative tests. The required spores were shaken dry from the leaves in Petri dishes, mixed intensively, and then used for the tests.

The method of Straib (1940) to spray the spores directly from the host plant to the germination substrate was rejected by me, since preliminary investigations had shown that the spores can be distributed in this way over the substrate surface in only a very irregular manner; consequently, the germination numbers may show great deviations within several parallel starts with material of the same origin. Better results were obtained by my method, according to which traces were taken from the spore collections mixed in the Petri dishes with a fine hairbrush and by which these traces were sprayed on the substrate by knocking them off over the cups. In this way the spores were evenly distributed in a satisfactory manner, and the germination developed more uniformly within the parallel tests with material of the same origin.

Larger quantities of spores from the field were required for various investigations. For this purpose I artificially injected highly sensitive wheat and barley types on the test field. During one test year only one race was propagated on wheat and barley, respectively. A mixture of the two races with each other or with foreign origins was not observed during the controls, which were made repeatedly.

Freshly sporulating leaves were cut off to obtain spores from field plants. The already existing spores were flushed with distilled water; after removal of the water the leaves were put into humid chambers, and these chambers were put up in the greenhouse. The spores newly formed within one to two days were then utilized for testing.

I did not use conserved spores or spore material which had been kept for a long time.

Other details of the method will be indicated in the text if required.

III. EXPERIMENTAL PART

A. MORPHOLOGICAL INVESTIGATIONS

1. Size of Uredospores

No uniform system can be obtained from the data given by various authors concerning the dimensions of uredospores of stripe rust. Table 1 gives the dimensions of uredospores formed on grain as published by various authors. The figures are possibly not always findings obtained on the basis of my own measurements.

From among the findings, some of which deviate from each other to a great extent, the values indicated by Straib (1941) are striking. In the measurements effected with different races he found, on the average, an unusual size of approximately $31 \mu \times 27 \mu$, and with a race originating from rye even a size of $34.7 \mu \times 29.3 \mu$.

I have measured spores of different races in order to clarify these contradictions and to check to what extent the measuring values depend on the various bedding media.

In most instances I have measured spores which have been formed in the greenhouse, to a limited extent material of race 24 from the field. All samples originated from freshly sporulating leaves. Two hundred spores were measured* of each

*The microscopic picture was projected with an eyepiece cup mirror on a plane, adjusted to 500-x enlargement, calibrated and then measured. The accuracy of the measurement was 11μ .

race or specimen, respectively; the various values were averaged and the dispersion (mean square deviation) was computed.

Table 1

Dimensions (in μ) of Uredospores of Stripe Rust on Grain According to Data Obtained from Various Authors

Author	Host Plant	Length of Spores	Width of Spores	Remarks
Eriksson and Henning, 1896	-	appr. 30	appr. 25	no precise data available
Evans, 1907	-	appr. 30	appr. 25	see above
Klebahn, 1914	-	22-25	17-22	
Allen, 1928	Triticum vulgare	22.5	17.4	
Arthur, 1934	-	19-30	16-26	
Viennot-Bourgin, 1940/41	T. vulgare	23.2	18.2	
	T. aestivum	22.7	18.6	
	T. spelta	21.4	18.2	
	T. polonicum	22.5	20.7	
	T. dicoccum	23.3	17.4	
	T. durum	21.2	19.6	
	Hordeum vulgare	23.5	18.8	
Straib, 1941	T. dicoccum tri-coccum and Hordeum tetrastichum pallidum	31.9	27.4	race 2
	(same)	31.5	27.8	race 7
	H. tetrastichum pallidum	30.8	27.0	race 23
	"	31.6	27.2	race 48
	T. dicoccum tri-coccum and Secale sp.	34.7	29.3	race 34
Manners, 1950	Triticum sp.	24.5	18.4	race 6x
	Hordeum sp.	23.8	18.5	race 46

The spores were measured air-dry, lying freely on slides, or on a 2 % water agar in open germ cups (Table 2). Furthermore, comparative measurements were made in distilled water, glycerine, and lacto-phenol (Table 3).

Figure 1 shows the percentage-wise frequency distribution of the longitudinal and lateral dimensions of 300 spores of one field origin of the race 24 (see page 7).

Table 2

Average Dimensions (in μ) of Uredospores of Various Stripe Rust Races (greenhouse origin); Spores Air-dry and on 2 % Water Agar

Race	Air dry		on 2 % Water Agar	
	Length of Spores	Width of Spores	Length of Spores	Width of Spores
1	21.0 (± 1.3)	17.5 (± 1.1)	-	-
2 A	21.0 (± 1.2)	17.0 (± 1.2)	-	-
7 (Is)	20.9 (± 1.0)	17.6 (± 1.1)	30.1 (± 1.7)	27.2 (± 1.3)
8 (D)	20.6 (± 1.0)	17.3 (± 1.1)	-	-
20A (T)	20.8 (± 1.3)	17.6 (± 1.2)	-	-
23	20.7 (± 1.4)	17.3 (± 1.0)	30.7 (± 1.9)	27.0 (± 1.7)
26	21.0 (± 1.1)	17.1 (± 1.2)	31.0 (± 1.8)	27.5 (± 1.4)
42A	20.2 (± 1.3)	17.0 (± 1.2)	-	-
54	20.2 (± 1.2)	17.2 (± 1.0)	30.7 (± 1.5)	27.0 (± 1.3)

Table 3

Average Dimensions (in μ) of Uredospores on Various Substrates; Stripe Rust Race 24 (field origin)

Substrate	Length of Spores	Width of Spores
Air	21.7 (± 1.5)	17.7 (± 1.6)
Glycerine (free from H_2O)	21.6 (± 1.6)	17.6 (± 1.7)
Lacto-phenol	23.9 (± 1.7)	20.1 (± 1.4)
Water agar, 2 %	30.9 (± 1.4)	27.3 (± 1.3)
Distilled water	31.1 (± 1.5)	27.7 (± 1.3)

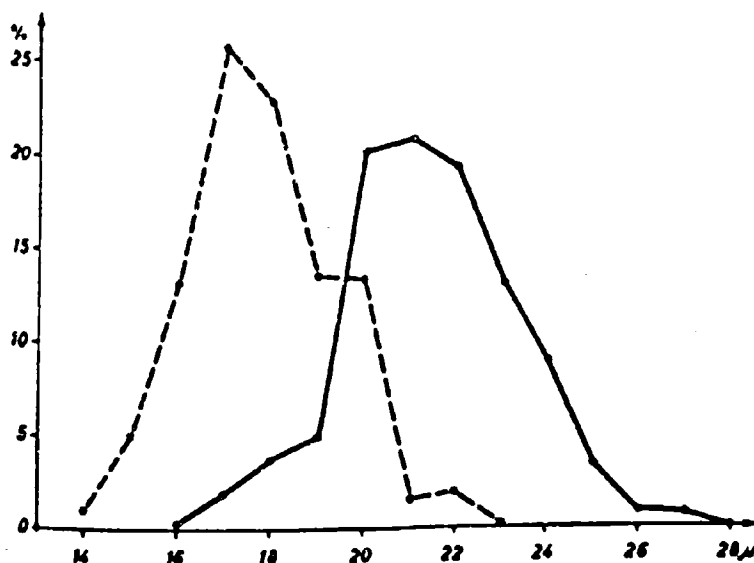


Figure 1. Frequency distribution of longitudinal and lateral dimensions of uredospores of stripe rust race 24 (field origin) in percentages; measured air-dry.

————— Length of spores
 - - - - - Width of spores

As was expected, the investigations have brought the following results: the values computed are largely determined by the substrate on which the spores are measured. On water or water-containing substrate the spores swell very fast and to a great extent, as had been observed by Allen (1928) and been pointed out by same. The greatly deviating findings of Straib (1941) can, therefore, be explained without difficulty, since he made his measurements on 2 % water agar. I obtained approximately the same values when I used this method.

The dimensions of the uredospores of stripe rust originating from wheat or barley are, measured air-dry, on the average approximately $20.8 \mu \times 17.3 \mu (\pm 1.2)$; in all cases measurement of spores made on several races at different times of the year (April and October) resulted in almost the same results.

The frequency distribution of spore dimensions shows that the highest frequency of the actual longitudinal and lateral

dimensions coincides approximately with the computed average values (Figure 1 and unpublished data).

The dispersion is -- in any case with the fresh spore material -- lower on the average than indicated by some authors (for instance, Gäumann, 1959).

A. 2. The Growth Pattern of Germ Tubes

In his efforts to find new additional methods of evidence for the identification of physiological races of stripe rust, Straib (1937, 1939a, 1939b, 1940, 1941) arrived at the conclusion that pathogenically different stripe rust races could be characterized also to a certain extent morphologically inasmuch as certain growth patterns of the uredospore germ tube are characteristic of them.

In numerous repeated tests he examined the germination of approximately 40 stripe rust races under defined conditions on artificial substrate. The following results were obtained: with regard to their germ tube growth the races can be divided into two main groups. The first group included the majority of wheat, and the few rye, stripe rust races; the second group includes most of the barley stripe rust races*.

Under certain test conditions the germ tubes of the uredospores grew more or less rectilinearly in the first group; at most they were slightly undulated, whereas a wavy and crimpy growth of the germ tube was characteristic of the second group. Still, final differences were obtained within these two groups with regard to the germination pattern of various races, for instance, between the barley stripe rust races 23 and 24.

According to Straib's observations the pattern of the germ tube growth is hereditary. However, it may be influenced, at the same time, to a greater or lesser extent, by environmental factors. In the first place the temperature -- during the start of cultivation of the spores and during the actual germination stage -- acts on the germination pattern. Thus, Straib found at low starting and low germination temperatures (2 to 5° C) that wheat stripe rust races developed wavy germ tubes also and that it was difficult to distinguish them safely.

*The designation "wheat stripe rust races," etc., means that they are races which fructify preferably on wheat, rye, or barley.

On the other hand, higher germination temperatures (about 20° and above), provided there was a germination here at all, effected a greatly elongated growth of germ tube, that is, the typical waves of various races otherwise established at lower germination temperatures were no longer present*.

Finally, Straib found a few specific wheat stripe rust races whose germ tube was very similar to that of barley stripe rust, also under normal start of cultivation and germination conditions, as well as a barley stripe rust race which stood out on account of an absence of swelling of the germ tubes.

Jointly with the statement that the pattern of germ tube growth can be greatly modified by temperature conditions (start of cultivation or germination temperatures), these observations left doubts with regard to the reliability of such a method of differentiation for races. This applies particularly to cases where differences in the manner of germination of the uredospore origins had been used to designate and name new races (Straib, 1939a).

However, additional possibilities of racial characterization are precisely desirable in the case of stripe rust as before, since the frequently fluctuating reactions to sowing on different types of material used in the tests and the lack of such materials make possible a further differentiation, which makes the analysis of the races difficult. Therefore, the usability of the method applied by Straib was again examined with a greater number of races because this point had not been analyzed thoroughly by other authors in the past.

Approximately 25 stripe rust races were checked, which had been isolated and taken from material sent from many different countries. Moreover, the uredoclonic material of further specific barley and wheat origins were examined, the classification of which in terms of races was still open.

The races and origins were cultivated under normal greenhouse conditions at approximately 15° C (it was not possible to examine the effect of low temperatures applied at the start of cultivation because rooms with correspondingly low temperatures were not available at the time of the examinations). The spore material came mainly from Triticum dicoccum tricoccum and

*Straib (1939b) was able to establish that changes in temperature influence the shape of the germ tube in the case of other types of grain rust also.

Hordeum tetrastichum pallidum (barley of Fong Tien). Besides this, the races were kept on several other types in order to be able to control the influence of the host plant. As far as possible, I have also included field material of various races. The following germination substrates were used:

1. Water agar, 0.5 to 2%; pH approximately 6.0 to 6.2 (not corrected) and with graded pH values of 3 to 11 (n/10 HCl or n/10 NaOH being used);
2. Gelatin, 2 to 5%; pH 5.6 to 6.5;
3. Silicic gel, approximately 3 to 5%; pH 5.0 to 6.0;
4. Distilled water.

Every germ cup was sowed with several hundred spores, put up in the dark, thermostat at constant temperatures, and the germ pattern was observed after approximately 5 and 24 hours.

Each race was tested several times, on the average over ten uredo generations; in individual cases it was possible to observe races over a period of two years. The results are compiled in Table 4.

The investigations had the following results:

As Straib found out, the germ tube growth of the races is apparently fixed genetically, however, it is greatly modified by outside factors, particularly temperature influences. Characteristic influences in the pattern of the germ tube growth between the various races can be determined with certainty at temperatures of approximately 8 to 15° C. These differences appear less clear if the spores germinate at very low or higher temperatures (below 5° C or around 20° C and above).

It was possible to observe the germ tube pattern typical for the different races in all substrates used. Only in the more alkaline and acid range (with agar substrates: pH smaller than 9 and greater than 4.5) does the pH influence the germination pattern in an unfavorable manner, that is to say, the growth forms of the germ tubes become generally atypical (great shortening and irregular swellings, partly with lateral branches of the germ tube).

Comparative investigations of greenhouse and field material of the same races showed in all cases an agreement of the germ tube growth pattern.

It was further found that the germ tube growth pattern depends also on the age of the spores -- sufficient germination capacity being taken for granted.

The uredospores of all stripe rust races generally form only one germ tube which has no branches in the normal case. Lateral branches may develop particularly at extreme germination temperatures and, as mentioned, with extreme pH values; the tendency in this direction seems to be different in the various races, but not to be constant enough to utilize this as a differentiating criterion.

Table 4

The Germ Tube Growth Pattern of a Few
Stripe Rust Races

Type of Growth *	Races	Type of Hosts
I	1, 2 (GB), 2 A, 7 (F) 7 (Is), 11 (Ke), 20A (F) 20 A (Ke), 26, 27/53, 32 A (Sz), 54 (D), 54 (NL) 55 (F), 55 (Sz), 58	Triticum
I a	8 (D), 20 A (D)	Triticum
I b	20 A (Gr), 20 A (T), 42 A	Triticum
II a	23	Hordeum
II b	24	Hordeum

- *I = Germ tube † rectilinear (Illustration 1)
 I a = Germ tube, slightly crimped
 I b = Germ tube, clearly crimped (Illustration 2)
 II a = Germ tube, with regular waves (Illustration 3)
 II b = Germ tube † irregular waves (Illustration 4)



Abb. 1, Rasse 54



Abb. 2, Rasse 42 A



Abb. 1, Rasse 54



Abb. 2, Rasse 42 A

Illustrations 1 to 4:

Germinated uredospores of stripe rust races of different germ tube growth types; on 2 % water agar, germination at 10° C.

Germination stage:

Illustrations 1, 3, 4: 5 hours after sowing;

Illustration 2 : 7 hours after sowing.

All photos: Ultraphot (Zeiss); approximately 140 x.

Illustration 1, Race 54

Illustration 2, Race 42 A

Illustration 3, Race 23

Illustration 4, Race 24

The majority of the specific wheat stripe rust races develop a more or less rectilinear germ tube, mean start of cultivation temperatures, germination at medium temperatures (approximately 8 to 15° C) and a suitable germination medium (for instance, agar substrates with pH values not below 4.5 and not above 9) being a premise (Illustration 1). Deviations from this type of growth were found in the races 8 (D), 20 A (D), 20 A (Gr), 20 A (T) and 42 A (Table 4 and Illustration 2). However, the deviations were never so great that the type of growth of a barley stripe rust race would have appeared. The differences in germination within the race group 20 A were striking, although with these origins an agreement between the reaction to affection was observed on the test specimen (physiological differences in germination within this group will be discussed at a later date).

The shape of the germ tubes of the typical barley stripe rust races 23 and 24 (Illustrations 3 and 4) contrasts very clearly with the growth form of wheat stripe rust races which is the type most commonly observed. The germ tubes are greatly undulated among the barley yellow host races. There is a morphological difference between the races 23 and 24 which has been described by Straib: the swelling of the germ tubes is clearly more narrow in race 23 and more uniform than in race 24. A barley stripe rust race, which showed the characteristic growth pattern for wheat stripe rust, was not found.

In twelve barley and wheat stripe rust origins from Japan whose racial classification has had to remain an open question up to the present time, all barley origins showed greatly swollen germ tubes, similar to the races 23 and 24, whereas the wheat origins showed the germination pattern known from most of the European wheat stripe rust races or, in one case, the growth pattern of the race 42 A which also comes from Japan.

It was possible to confirm the statement made by Straib that the germ tubes of the barley stripe rust races decompose on artificial substrates faster than those of wheat stripe rust.

A. 3. The Formation of Vesicles and Secondary Hyphae

Sometimes, one or two bubble-like swellings (vesicles) develop on artificial germination substrates in various types of rust, at the apical part of the uredo germ tube one or several "secondary" hyphae developing from the final small bubbles. These phenomena have been described several times in literature some time ago (Sappin-Trouffy, 1896; Arthur, 1929; Ezekiel, 1930). In more recent times the formation of vesicles, particularly with the types of grain rust, were examined by various authors (for literature see Table 5). Very different factors seemed to release or favor the formation of vesicles. On the other hand, the formation of the (secondary) vesicles is said to be characteristic under defined conditions on certain agar substrates for each of the types of rust examined by them, according to Hurd-Karrer and Rodenhiser (1947).

These vesicles developing on artificial germ media and the secondary hyphae claim special interest because they are similar to certain formations appearing in vivo. However, up to the present time we cannot say with safety to which structures which develop during the course of the infection they are homologous, and whether this applies at all. The various authors have expressed different views on this point. I will not go into more detail with regard to these purely hypothetical statements.

Table 5

The Development of Vesicles and Secondary Hyphae in
Different Types of Rust on Artificial
Germination Substrates

Author	Type of Rust	Encouragement of Vesicle Formation by
Straib, 1940	<i>P.striiformis</i>	Fructification at high temperature; higher acidity of the substrate (pH 4.5)
Hurd-Karrer and Rodenhiser, 1947	<i>P.graminis tritici</i> <i>P.recondita tritici</i> u.a.	Glucose mineral salt - agar
Dickinson, 1949	<i>P.recondita tritici</i> u.a.	Paraffin collodium membranes ("contact-stimulus")
Manners, 1950 Sharp and Smith, 1952	<i>P.striiformis</i> <i>P.coronata</i>	- Zn salts, depending upon pH
Sharp, 1954 Allen, 1957	<i>P.coronata</i> <i>P.graminis tritici</i>	Zn salts and silicon Distillate from aqueous uredospore extracts
French and Weintraub, 1957	<i>P.graminis tritici</i>	Pelargonaldehyde
Fuchs and Gaertner, 1958	<i>P.graminis tritici</i>	Silicic gel nutrient media, certain amino acids
Emge, 1958	<i>P.graminis tritici</i>	defined light and temperature combinations
Naito et al., 1960	<i>P.coronata</i> <i>Uromyces alopecuri</i>	Peptone-salt-agar
Couey and Smith, 1961	<i>P.coronata</i>	Cation effects (Zn-H-Ca-Mg)
Pavgi and Dickson, 1961	<i>P.sorghii</i>	Cellophane membranes, certain light and temperature conditions

In my investigations in which I used a substrate mainly water agar (1 to 2%) or gelatine (3 to 5%) with pH values between 5.5 and 6.5, I was able to observe the following:

If the spores had been formed at medium temperatures (around 15° C) and if the germination temperature was approximately 10° C, vesicles developed only occasionally (with less than 1% of the germinated spores) [also with Manners, 1950]. However, if I left the spores to germinate at temperatures of 10° C after an initial cultivation temperature of approximately 20 to 25° C, the basic formation was clearly encouraged (up to 12%), as has also been observed by Straib.

Now, for the first time, I was able to state, also in the reverse case, that with a medium start of cultivation and higher germination temperature, an increased formation of vesicles occurred. Thus, with various races vesicles and secondary hyphae showed up to 10% of the germinated spores, if they germinated after a fructification temperature of 15° C at approximately 20° C.

A still greater encouragement of vesicle formation was obtained through the utilization of phosphate-buffered silica gels with a pH value of 5.0 to 6.0 (method according to Fuchs and Gaertner, 1958). On these germination soils and at temperatures around 10° C, up to 30% of the germinated spores formed vesicles, partly with secondary hyphae, here again a high fructification temperature favoring their formation.

An encouragement of basic formation by a higher degree of acidity of the agar substrate (pH 4.5), as indicated by Straib, was not ascertained by me. It is true, striking bubble-like irregular swellings (without secondary hyphae) are formed on such substrates along the germ tube; however, they are abnormal phenomena and have probably nothing to do with a vesicle.

In general, the tendency for the formation of vesicles is greater with barley stripe rust races than with most wheat stripe rust races. This observation was also made by Straib. On the other hand, the shape and size of the vesicles as well as the number and growth of the secondary hyphae are the same with all races examined.

Depending upon the germination rate, the vesicle formation starts approximately 6 to 24 hours after start of germination. In this case, the germ tube attains only a length of a few hundred μ , whereas normally lengths of thousand μ and more develop. Typical for all examined races is that only one clearly formed vesicle developed which often attains the size of a uredospore.

The number of secondary hyphae is mostly 1 to 2, in rare cases 3 to 4. The plasmatic content of the germ tube concentrates after formation of the vesicles in it and also in the secondary hyphae if same are formed.

A vesicle formation typical for stripe rust with secondary hyphae is shown in Illustration 5.

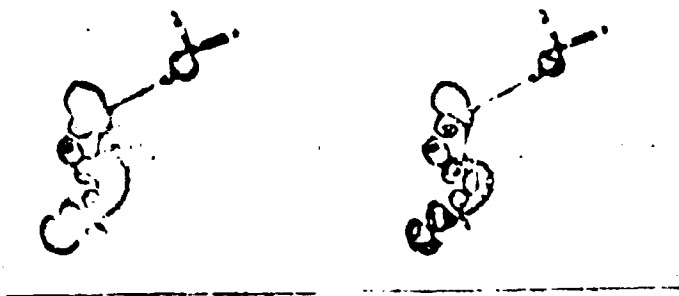


Illustration 5

Germinated uredospores (stripe rust race 24); germ tube (collapsed) with final vesicle and two secondary hyphae (on the left partly not germinated spores).

Photograph approximately 24 hours after seeding on 2 % water agar; Ultraphot (Zeiss); 200 x.

Different variations of this type may develop. Straib (1940, pages 218 to 221) has published a number of drawings of such variations of growth.

An increased growth of the secondary hyphae resulting from the vesicles was not achieved with any stripe rust race in the same manner as Fuchs and Gaertner (1958) had obtained with P. graminis tritici by adding a nutrient solution according to Knop, various amino acids, native chicken egg yolk, pyridoxin and Fe compounds. Also an addition of sterile filtered coconut milk to silicic gel nutrient media (Gaertner and Fuchs, 1960) and the application of glucose mineral salt agar according to Hurd-Karrer and Rodenhiser (1947) did not clearly encourage the growths of secondary hyphae or of germ tubes.

Remarkable is the relatively long life of the vesicles and secondary hyphae which was pointed out by Straib. Whereas the normal germ tube starts to decompose usually after 1 to 2 days, the vesicles and the secondary hyphae may remain intact for a week and longer periods depending upon the temperature of germination period. The secondary hyphae continue to grow slowly under favorable germination conditions during the first days after their formation; however, in most cases only lengths of 100 to 200 μ were observed. In very few cases they attained a length of approximately 400 μ .

Besides the checking on agar or gelatin I have for the first time gone into the question of vesicle formation in vivo; I was able to establish such structures repeatedly on the surface of the leaf. As was mentioned high germination temperatures favored the formation of vesicles on artificial substrate. Apparently their formation is also encouraged in the germination in vivo by higher temperatures or initiated as such. Thus, I was able to observe frequently on germination leaves and leaves of all stages of various wheat and barley types which had been inoculated with uredospores of individual stripe rust races, that the germ tubes had formed vesicles and secondary hyphae on the surface of the leaf if the incubation temperature was 20° and over. These structures appeared at random on the epidermis of the leaf and not preferably at the stoma of the leaves.

This observation is remarkable insofar as it will probably lead ad absurdum all those speculations which want to see homologues to the structures in the vesicles which develop only after infection within the host tissue. But also the assumption that the vesicles developing in vitro are formations which would correspond to an appressorium cannot be maintained. The question whether P. striiformis forms an appressorium or not is disputed as such. Thus, Eriksson and Kenning (1896) mention that the germinating stripe rust spores formed appressoria on grain leaves. Also Evans (1907) indicates an appressorium with the stripe rust which, however, he designated as a "not very definite structure." On the other hand, Marryat (1907) and Allen (1928) found that the germ tubes penetrated into the stomata without forming appressoria. Particularly Allen, who examined the process of infection with the stripe rust histologically in very great detail, pointed out the lacking formation of appressoria as a characteristic criterion of stripe rust.

I have gone into this point again. Whereas Allen made her examinations on fixed and colored cuts, I produced complete preparations because the main point was only the investigation

of the germination and the primary infection process on the leaf*.

It was found that regardless of race, host and germination conditions, the germination tubes always penetrated into the stoma openings of the host plants without forming a marked appressorium.

Comparative observations on P. recondita tritici showed, on the other hand, a clear formation of appressoria of the germination tubes, under the same germination conditions, above the stoma openings of the inoculated wheat leaves.

B. GERMINATION PHYSIOLOGICAL INVESTIGATIONS

Whereas all previous physiological investigations on germination with the stripe rust and other grain rust types were made without the knowledge of the physiological specialization and, consequently, hardly permitted a binding statement, Wilhelm (1931) and Stroede (1933) used for the first times specific cases of stripe rust. However, they were not able to find any differences between the various races. On the other hand, Straib (1937, 1939a,b, 1940, 1941) managed to establish clear differences with the investigation of a great number of races, with regard to their germination reaction to artificial substrate. As was mentioned, these differences showed morphologically in the growth pattern of the uredo germ tubes (see paragraph A. 2) and physiologically in the reaction to various environmental factors. Particularly impressive was the statement made by Straib that certain outside factors such as light

*An aqueous uredospore suspension was spread on germination leaves and leaves of all stages (also of field plants). I used wheat and barley types of the stripe rust test assortment which were highly sensitive or \pm resistant for the race under examination in the case concerned. The growth layer of the leaves was removed prior to inoculation, or left. After the inoculation the plants were put into humid chambers (daylight or absolute darkness, temperatures constant 5°, 10°, 15°, 20° C or fluctuating between 15 to 25° C). The inoculated leaves were cut off after the various periods of incubation (at the earliest after 4, at the latest after 28 hours) and then they were fixed up to the decoloration of the leaf tissue (ethanol 50 % 90, glacial acetic acid 5, formaldehyde 5 parts by volume). Then they were dyed with a solution of 0.05 % trypanblue in lactophenol (dyeing period approximately 5 minutes).

and temperature, are able to clearly modify the subsequent germination reaction as early as during the formation of the spores on the host plants. These influences had previously never been taken into account or, as was the case in the pertinent investigations made by Becker (1928) or Wilhelm (1931), had not been clarified in a satisfactory manner.

In view of the infection findings always observed in the work with stripe rust, which contradict all experience, it appeared necessary to examine again the germination process of a great number of stripe rust races under different conditions.

1.a) The effect of various agar types and concentrations on germination

According to the statements made by Wilhelm, Stroede, Straib, and others a solid water agar is more suitable for germination tests with stripe rust uredospores than a liquid substrate. Spores which are on a solid substrate can be distributed in a more even manner; subsequently, it is also easier to sort and count them because the germination tubes which are on liquid media rise from the substrate into the air. Moreover, Straib obtained only a very slight germination on tap water and distilled water, but normal germination on rain water.

Remarkable is the observation made by Manners (1950) according to which differences in germination of a stripe rust race may result from the use of different agar qualities under otherwise identical germination conditions*.

Should the stripe rust really show a noticeable reaction to such differences of substrate, the indicativeness of all germination tests is made doubtful insofar as they have not taken into account this factor. In the same way the statements made by Wilhelm and Straib could be generalized without difficulty according to which a 5 -- 6% water agar results in a better germination than 1.5 -- 2% or according to which the germination rate (speed) is higher on 5 -- 6% agar than on agar of low concentration (Wilhelm, 1931).

To clarify these points I have made a number of experiments. The germination tests were carried out in Petri dishes

*Significant differences with regard to the development of the process of germination were ascertained in germination tests with conidia of Peronospora tabacina when different agar origins were used (Shepherd, 1962).

(diameter of 5 centimeters) and, unless special effect of light were to be examined, in the dark under thermostatic check. Prior to the introduction of the tests I have always brought the germination dishes to the temperature to be examined. Every test was repeated with three parallels 2 to 3 times. The germination percentages were ascertained per germination dish for 200 spores, the mean values were calculated and with the various specimens the total germination pattern was compared with the computed values (more than 1000 uredospores were sprayed on each germination dish).

To test the effect of the substrate I have first examined, in a comparative manner, several stripe rust races on Difco-Bacto- and Merck water agar (purified agar for nutrient media; Merck Company).

All races germinated on Merck agar always faster and often also more completely than on Difco agar of the same concentration (Table 6 and Figure 2).

Table 6

The Effect of Various Agar Substrates on the Germination (in %) of the Uredospores of Stripe Rust Races; Germination Temperature 10° C; Germination Percentages after 4 Hours*

Race	Merck agar (1 %)	Difco agar (1 %)
1	65	3
7 (Is)	98	52
20 A (T)	64	10
54	83	50

*After 24 hours all races on both agar substrates had germinated to an extent of 90 to 100%.

In germination tests with stripe rust races which sporulated under unfavorable conditions in the season of the year with little light, also the final germination values on Difco agar were considerably lower than those on Merck agar. Thus, for instance, a race showed 77% germination on a 1 % Merck agar on January 23, 1963 after 28 hours (and after 3 days)

under the optimal germination temperature of 10° C, but only a 14 % germination on a 1 % Difco agar.

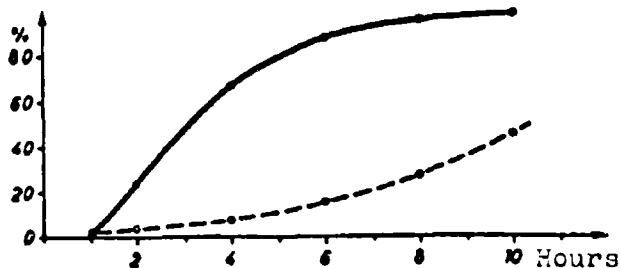


Figure 2. Germination of uredospores of the stripe rust race 26 on different agar substrates; germination temperature 10° C.

———— "Merck" agar (2 % water agar)
 - - - - "Difco-Bacto" agar (2 % water agar)

Furthermore, striking differences were noticed with regard to the germination reaction on agar soils after the use of unwatered and watered* fiber agar (quality DAB 6.):

On a substrate which had been obtained with unwashed fiber agar, the stripe rust spores germinated much faster than on substrates which had been prepared with previously watered agar of the same origin (Table 7).

I was not able to confirm the statement made by other authors, mentioned at the beginning, according to which the stripe rust uredospores germinated faster or better on 5 to 6 % water agar than on 1 to 2 %. Both with the utilization of Difco as well as with the utilization of Merck agar it was found that the germination of agar substrates of lower concentration (0.5 %) developed clearly at a faster rate than of those of higher agar concentrations (2 and 5 %); on the other hand, no differences were found between the various final germination values. As an example I have given a germination test on Difco agar of different concentration in Table 8.

*Finely cut, washed 48 hours in flowing subsequently distilled water, and air-dried again.

Table 7

Germination (in %) of Uredospores of the Stripe Rust
Race 27/53 on a 2 % Water Agar upon Use of
Fiber Agar (DAB 6.)

a = untreated agar, b = watered agar*

Germination time in hours	Germination temperature 10°C		Germination temperature 17°C	
	a	b	a	b
5	62	11	6	0
7	87	14	15	1
24	95	95	90	60

*Finely cut, washed 48 hours in flowing subsequently distilled water, and air-dried again.

Table 8

Germination (in %) of Uredospores of the Stripe Rust
Race 26 at 10° C on Difco Agar of Different Concentrations

Germination			
After hours	on agar concentrations of		
	0.5 %	2 %	5 %
3	16	1	0
5	43	12	3
8	88	47	22
24	96	95	92

Furthermore, I was not able to confirm the statement made by Straib, according to which the stripe rust spores germinate only slightly on tap water or distilled water. The spores of several stripe rust races germinated equally well on distilled

water as on solid water agar, the racial differences being parallel on both substrates (Table 9).

Table 9

Germination (in %) of the Uredospores of Different Stripe Rust Races on Distilled Water and 1 % Water Agar (Merck) at 10° C after 24 Hours

Substrate	Germination of Race			
	2 A	7 (Is)	26	55(Sz)
Distilled water	25	97	98	7
Water agar (1 %)	23	97	100	8

In the same manner, tap water (total hardness 3.2 -- 3.5 D.H.; pH 5 to 6) proved a suitable germination medium (rain-water was not tested).

However, a premise for the germination on liquid substrate was in each case that the spores were thinly distributed (approximately 0.5 to 1 mg/3 ml of water in germination dishes of a diameter of 5 centimeters) on the water surface because immersed spores, as is known, do not germinate (for literature see Becker, 1928).

A separate investigation was made on the significance of the hydrogen ion concentrations (see page 26).

On the basis of these results of the investigation I used, unless special substrate influences were to be examined, a 1 % Merck agar in all other germination tests, which was always prepared freshly with distilled water.

The striking observation may here be registered according to which in tests with uredospores of different races of P. recondita tritici differences of influence of various agar types on the process of germination were not observed. Both on Difco and Merck agar, on washed and untreated fiber agar, the brown rust spores had finished germinating already after three hours in all cases to the extent of more than 90 %.

1.b) The effect of different gelatin substrates on germination

Various authors have used gelatin also for germination tests with uredospores of various rust types, with different evaluation. Thus, Loegering (1941) observed that the uredospores of P. graminis tritici germinated on gelatin substrates of various concentrations less well than on water agar. Sharp and Smith (1952), on the other hand, found that a 3 % gelatin is very suitable for germination of P. coronata avenae. More precise literature references concerning the suitability of gelatin substrates for germination tests with stripe rust races are not available as far as I know. Therefore, I examined also the effect of gelatin types. The following types of gelatin were tested: Difco-Bacto gelatin, purified gelatin for nutrient media (Merck) and an unpurified type of gelatin. Of these types always a 3 % substrate was prepared with distilled water. The pH was with

Difco-Bacto gelatin	(3 %)	6.4
Unpurified gelatin	(3 %)	5.6
Merck gelatin	(3 %)	4.3

Table 10 shows the development of the process of germination of the uredospores of three different stripe rust races on these substrates.

Table 10

Germination (in %) of the Uredospores of Stripe Rust Races on 3 % Gelatin Media; Germination Temperature 10° C

Race	Germination on								
	Difco gelatin 3 %			Unpurified gelatin 3 %			Merck gelatin 3 %		
	3hrs.	6hrs.	24hrs.	3hrs.	6hrs.	24hrs.	3hrs.	6hrs.	24hrs.
7 (Is)	41	79	100	33	78	98	0	4	85
26	60	85	100	40	76	100	1	6	88
55 (Sz)	0	1	2	0	1	3	0	0	0

It was found that the races 7 (Is) and 26, as well as a few other stripe rust races which are not listed here, finished germinating almost completely on Difco gelatin and unpurified gelatin, the germination rate on Difco gelatin being higher than on the other gelatin substrates. It is true high

germination percentages were achieved on Merck gelatin with these races; however, the germination rate (speed) was considerably lower than on the other substrates. Above all, the longitudinal growth of the germ tubes (also with other races) was greatly retarded on Merck gelatin, which is not shown by the table. The germ tubes reached only lengths of a maximum of 300 μ on Merck gelatin soils whereas, on the other gelatin substrates, the germ tubes lengths of more than 1000 μ were measured.

The reason for this retardation on Merck gelatin is probably mainly explained by the relatively high acid reaction of the substrate (pH 4.3). However, with other experiments also on Merck gelatin with a corrected pH value (5.0 minus 6.5; addition of phosphate buffers or n/10 NaOH) a significant although slightly lower retardation of the growth of the germ tubes was observed.

In race 55 (Sz) no germination appeared on the Merck gelatin at all. However, the uredospores of this race also germinated only in traces on the other gelatin origins. The strikingly low germination of this race was always found again in my subsequent numerous experiments regardless of whether gelatin or agar substrates were concerned.

In further tests the impact of various gelatin concentrations on the germination was examined. In concentrations of 2 to 10 % no difference of effect was found within the same gelatin type on the germination of the tested races.

However, in the simultaneous testing of suitable gelatin and agar substrates, it was found that the germination of one and the same spore origin was to a great extent the same on both substrates. As was already mentioned (compare Paragraph A. 2) the growth pattern of the germ tubes characteristic for certain stripe rust races was identical under the same temperature conditions, on gelatin substrates (with the exception of Merck gelatin) and on agar. However, agar substrates are more suitable for comparative germination tests than gelatin soils because in the latter, above all at high temperatures (around 20° C), a liquidation (thinning) occurs frequently (decomposition of gelatin on account of various bacteria brought in) and thereby the germination of stripe rust spores is greatly impaired.

With repeated germination tests with uredospores of P. recondita tritici which were carried out parallel to the germination tests with stripe rust spores (at 10 to 15° C), it was observed that the wheat brown rust spores had finished germinating on all three types of gelatin used already after three hours to the extent of more than 90 %. Here it was again

found that the uredospores of the brown rust do not react to different substrate influences in the same manner as the stripe rust spores. However, a reservation must be made: the longitudinal growth of the germ tubes of brown rust spores on Merck gelatin (pH 4.3) is clearly smaller than on other types of gelatin, similar to the stripe rust.

1.c) Effect of hydrogen ion concentrations on germination

The effect of various hydrogen ion concentrations on the germination of stripe rust uredospores was so far exclusively analyzed by Straib (1940) with several stripe rust races. Therefore, it was desirable to check his findings and to supplement them. Among others it was necessary to examine the effect of different substrates and ions in connection with the pH effect of the stripe rust.

In his experiments Straib had used a 2 % water agar and the various pH values were set by adding n/10 HCl or NaOH to the water of the solution. I used the same method*.

However, for the test series I used only a 1 % water agar (Merck) because no differences had resulted in the preliminary experiments in the germination values (after 24 hours) when the germination was tested on 1 or 2 % water agar. The germination specimens were put up at various temperatures, always in the dark thermostat. Germination temperatures around 10° C proved most suitable for comparative tests. The germination percentages were ascertained after 24 hours.

Figure 3 shows the germination of stripe rust races 2 A and 7 (Is) of 1 % agar with different pH. The two races germinated to a different extent; however, they showed a pH dependency which was in agreement. The minimum was in the acid range at pH 3.0, the optimal range between pH 5.0 and 7.0 and the germination limit in the alkaline range about pH 10.5 (measured 11.2).

*With the addition of NaOH (or KOH) to non-buffered water agar the pH drops, to a certain extent, at the beginning. Therefore, the spores were only sown on such substrates after an approximately constant pH had been achieved. In all substrates I ascertained the pH potentiometrically by using one-bar measuring chains (Schott Company) -- (Potentiometer: Freye Company; pH measuring range: 1 to 14; measuring accuracy: 0.1 pH).

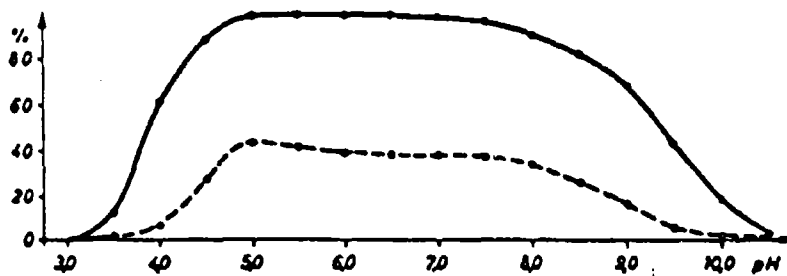


Figure 3. Germination of uredospores of the stripe rust races 2 A (—) and 7 (Is) (---) with different pH (for details see Text).

Straib found as a minimum a pH of 3.4 to 3.1 and an optimum of approximately 5.0 to 7.0 on a 2 % agar, depending upon the race. Thus, my data agree with the values found by Straib to a great extent. The limit of germination in the alkaline range was not ascertained by Straib. However, with a pH of 8.5 he still found fairly high germination percentages with the races tested by him.

Silica gels* of various pH values were also tested by him in order to clarify whether there is a relationship between the material condition of the substrate and the hydrogen ion concentration. As an inorganic and largely neutral substrate silica gel had proved suitable in germination tests with P. graminis tritici (Fuchs and Gaertner, 1958).

The results of germination tests with various stripe rust races on phosphate-buffered silica gels (pH 5.0 to 7.5) are given in Table 11.

*From an approximately 3 % Na silicate solution (Na silicate pure, dry; Merck Company) first silicic acid sol was obtained according to the method of Taylor (1950) -- (ion exchanger: Lewatit S 100; Bayer-Leverkusen Company). The aqueous clear silicic acid sol obtained in this manner had first a pH of approximately 2.8. By adding a basic phosphate salt solution (method according to Fuchs and Gaertner, 1958) clear silica gels were obtained, the pH values of which could be set accurately within the range of 5.0 to 7.5.

Table 11

Germination of Uredospores of a Few Stripe Rust Races
on Phosphate-Buffered Silica Gels of Different pH;
Germination Percentages after 24 Hours;
Germination Temperature 10° C

Substrate	Germination of Race		
	7 (Is)	23	54
Silica gel			
pH 5.0	95	96	92
pH 5.5	97	96	93
pH 6.0	70	66	63
pH 6.5	42	37	30
pH 7.0	33	20	15
pH 7.5	6	2	4
Water agar (1 %; pH 6.2)	96	95	97

In these tests which were repeated several times, it was always found that the uredospores of the tested races were able to fully germinate on silica gels within only a pH range from 5.0 to approximately 5.5. From a pH of approximately 6.0 on, clear germination depressions appeared on these substrates and with a pH of 7.5 all races germinated as traces only. This was observed particularly clearly in tests which were conducted with a spore material under unfavorable conditions, during a season with little light. Here the spores germinated already with a pH of 6.5 only to a very slight extent (less than 10%).

Also on silica gels which had been prepared by precipitation of silicic acid sol with n/10 NaOH/NaCl, the stripe rust spores germinated as on phosphate-buffered silica gels, that is, here again the germination diminished considerably from a pH of 6.0 on.

In parallel germination tests of stripe rust spores on 1 % water agar which was adjusted by an addition of n/10 HCl or n/10 NaOH to a different pH value, and on silica gels of the same pH levels (addition of n/10 NaOH/NaCl or basic phosphate salt solution), it was possible to ascertain that the optimum pH for the germination, in accordance with the above-mentioned data on agar, is much broader than on silica gel. The graphic presentation of the results of germination tests with spores of race 26 shows this clearly (Figure 4).

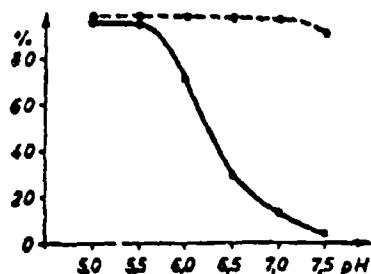


Figure 4. The germination of uredospores of the stripe rust race 26 (at 10° C) on agar and silica gel substrates of different pH; germination percentages after 24 hours.

- - - - - = water agar, 1 %
(Merck), pH adjustment by adding n/10 HCl and n/10 NaOH.

————— = silica gel, pH adjustment by adding n/10 NaOH/NaCl

The reason for the germination quotas on silica gels dropping sharply at only a pH above 6.0 can probably be explained by the fact that relatively high concentrations of buffer salts or NaOH must be added in order to obtain from relatively acid silicic acid salts (pH 2.8) silica gels of slightly acid, neutral or slightly basic reaction. Such an assumption is supported by the results of germination test with various stripe rust races on 1 % water agar and distilled water in which potassium phosphate buffers or phosphate buffers according to Sørensen are used to adjust to certain pH values (for instance, 6.5): with a buffer salt concentration of 0.1 mole and even with 0.05 mole the spores germinated only slightly (approximately 20 to 35%), whereas the germination on both media with a buffer salt concentration of 0.01 mole normal developed in the same way as on the unbuffered control substrates (greater than 90%)*.

*Very similar observations were also made by Bell and Daly (1962) in germination tests with uredospores of Uromyces phaseoli on phosphate-buffered germination substrates.

Also with comparative germination tests on alkaline, partly unbuffered, partly buffered with 0.05 mole of glycol, 1 % agar soils which were adjusted to the same pH values by corresponding additions of n/10 NaOH, the germination was almost completely suppressed on the buffered substrates as a result of the relatively high concentration of NaOH already at a pH of 9.0 (0.05 mole of glycol alone did not inhibit the germination) whereas the uredospores on the unbuffered agar substrates (with a slight addition of NaOH) finished germinating with the same pH still to the extent of approximately 60 %.

I conducted the tests analyzed so far in which the effect of different pH values had been examined always at optimum germination temperature (10° C). In these tests a clear decrease of germination was ascertained with an increase in the acidity of agar substrates (approximately from a pH of 4.5 on) -- (it was possible to prepare and examine silica gels according to the above indicated method from only a pH of 5.0 on). According to Straib (1940), however, a relatively high acidity of the agar substrate may at the same time have a surprising effect: if, in his tests, stripe rust uredospores were sown at high temperatures (higher than 20° C) on a 2 % water agar acidified with n/10 HCl at a pH of 4.4 to 4.6, then the spores germinated more fully than on pure water agar (pH 6.0 to 6.2). This means that through the effect of the acid the germination depression, depending on the high temperature, was more or less compensated.

I have checked these statements made by Straib on several stripe rust races. As a substrate I again used 1 % water agar (Merck); a pH of 4.5 was set by adding n/10 HCl, diluted H₂SO₄ or HNO₃ to the agar solution, and the germination specimens were put on the various substrates at a temperature of 22° C.

The results of a test series made with the races 7 (Is) and 54 are given in Table 12.

These tests, which were repeated with other stripe rust races with the same results, lead to results quite similar to those obtained by Straib. In addition, it was found that diluted HNO₃ and H₂SO₄ had the same effect on the germination as HCl. This was also proven under different conditions: with a germination temperature of 10° C all three acids had the effect, without exception, of a delay of the relative germination rate, from a pH of 4.5 on, showing the same drop of the germination percentages and a smaller growth of the germ tube. The pH minimum of the germination was 3.0 to 3.5 in all tested acids.

Table 12

Influence of the Hydrogen Ion Concentration of Various Acids on the Germination of Uredospores of Stripe Rust Races at Higher Temperature (Substrate 1 % Water Agar; Germination Temperature 22° C; Germination Percentages after 24 Hours)

pH of the Substrates	Germination of the Race	
	7 (Is)	54
6.2 (Control)	4	6
4.5 (HCl)	73	68
4.5 (HNO ₃)	78	69
4.5 (H ₂ SO ₄)	71	75

The influence of these inorganic acids on the germination does thus not depend on their anions under the selected test conditions. A completely different picture was obtained with the use of an inorganic acid. Thus, I found, for example, that the germination was completely retarded with every race and at every temperature on agar substrates which had been adjusted by a small addition of pure acetic acid at a pH of 4.5 (0.02 % of acid added) or by a still higher acidity.

B. 2. The Effect of Outside Factors During the Formation of Spores on the Subsequent Germination Reaction

The development of the process of germination of the uredospores may be influenced by various outside factors which have an effect as early as during the fructification of the fungus (Becker, 1928; Wilhelm, 1931; Straib, 1940; Manners, 1950).

Some of the statements made by Wilhelm and Straib concerning the effect of various outside factors on the subsequent reaction of the uredospores in the germination process are completely divergent. Unfortunately, it is very difficult to compare the findings with each other since Wilhelm made his experiments with unusually slow germinating stripe rust spores, whereas Straib worked with spore material which germinated relatively fast and well.

2.a) Host plant

According to Straib (1940) the kinds on which the uredospores were formed had no specific effect on the subsequent reaction of the spores in germination.

In my test series which I conducted for more than two years, I was able to observe under very different germination conditions that again after simultaneous sporulation of a race on various wheat or barley kinds, the reaction of the uredospores in the germination was the same.

Also between spore origins of the same race which had been formed in the usual manner on germination plants or on leaf cuttings (leaf cultures of infected leaves on distilled water with and without the addition of 10 to 30 ppm benzimidazol or on a 1 to 5 % glucose solution) of different kinds of wheat, no evidence of differences in the reaction during the germination was established when the spores had been propagated at the same time and under the same temperature and light conditions.

2.b) Temperature

Eriksson and Henning (1896) were the first to find that the temperatures prevailing during the fructification of the stripe rust have a subsequent effect on the reaction of the uredospores during the germination. Subsequently, Wilhelm (1931) and particularly Straib (1940) have examined this phenomenon more closely. However, Straib arrived, in part, at entirely different results from Wilhelm. Whereas Wilhelm found that the uredospores of different races formed at low temperatures (below 10° C) did not germinate, Straib, on the other hand, established clearly that precisely a very low cultivation temperature (approximately 2° C) compared to the usual cultivation temperature of approximately 15° C strikingly stimulated the subsequent germination of the stripe rust spores. On the other hand, Straib observed that also particularly high fructification temperatures (higher than 20° C) could have a favorable effect on the germination capacity. However, the subsequent effects of the cultivation temperature were established only at specific germination temperatures.

I was not able to check the impact of extremely low fructification temperatures. However, as Straib, I have always observed that the germination of different stripe rust races was at least not smaller, after a cultivation at 8 to 10° C, than at a fructification temperature of 15° C, as maintained by Wilhelm. In agreement with Straib it was further found that high cultivation temperatures (around 20° C and above) increase the subsequent germination rate (particularly apparent at a

germination temperature of 10° C) and at the same time the maximum temperature of germination compared to those spores which had been formed at medium temperatures (around 15° C). This was found at different cultivation temperatures in the greenhouse (Table 13) and with a comparative germination process between spores of race 24 formed partly in the greenhouse at 15° C, partly outdoors* at high summer temperatures (maximum 29° C) on barley of Fong-Tien (Table 14).

Table 13

Effect of the Fructification Temperature on Subsequent Germination (in %) of the Uredospores of Stripe Rust Races (Substrate 1 % Water Agar)

Fructification temperature	Time of germination (in hours)	Germination of Race					
		7 (F)		20 A (T)		26	
		20°	25°	20°	25°	20°	25°
15°	3	0	0	1	0	0	0
20°		8	0	9	0	17	1
15°	30	2	0	3	0	17	0
20°		<u>32</u>	3	<u>20</u>	1	<u>53</u>	4

Table 14

Effect of the Fructification Temperature on Subsequent Germination (in %) of the Uredospores of the Stripe Rust Race 24 (Substrate 1 % Water Agar)

Culture in:	Germination at					
	10°		20°		29°	
	after 3 hrs.	after 24 hrs.	after 3 hrs.	after 24 hrs.	after 3 hrs.	after 24 hrs.
Green-house at 15° C	12	98	1	15	0	0
Outdoors at 18 -- 29° C	<u>65</u>	99	4	<u>94</u>	1	3

*The plants from the field were kept under shaded glass cases during the subsequent sporulation (1 day).

2.c) Humidity of air

Tests were made with regard to the influence of the relative humidity of the air during the fructification on the subsequent germination reaction of the stripe rust uredospores by Wilhelm (1931) and Straib (1940). These tests again led to completely different results. Thus, Wilhelm observed only a small germination (maximum of 15%) of the uredospores when same, several days previously, had remained on the host plants under a relative air humidity of 85%, whereas the spore biotypes of host plants which were kept under 55 -- 70% of pure humidity completed the germination to an extent of more than 90%. However, Straib found that precisely in this case the germination capability or rate of the uredospores was lower if the sporulation had taken place freely in the greenhouse instead of glass cases (pure humidity higher than 95%), at a relative air humidity of approximately 65 -- 70% and the sporulating germination plants had remained under these conditions for several days before the spores were brought to germination.

In my investigations I have put the infected host plants always under glass shields, with beginning sporulation, under which, due to humid potting soil and the moistened peat basis, an almost saturated atmosphere prevailed (pure humidity higher than 95%). This had in no way an unfavorable effect on the germination capacity of the uredospores. Thus, my observations agree with the findings of Straib. Moreover, I was able to confirm the statement made by Straib according to which the germination of spores which had been formed freely in the greenhouse (pure humidity 60 -- 65%) developed clearly at a slower pace compared to those spore biotypes which had been formed under the glass shields under a high air humidity (pure humidity higher than 95%) under otherwise the same conditions. However, no differences were found between the final germination values of the two series (Table 15).

Table 15

Effect of Air Humidity during Fructification at 15° C on Subsequent Germination (in %) of the Uredospores of Stripe Rust Races (Substrate 1 % Water Agar; Germination Temperature 10° C)

Relative Air Humidity During Fructification	Germination Time in Hours	Germination of Race		
		7 (Is)	26	54
60 - 65 %	3	35	20	24
	5	66	55	50
	24	100	100	98
Above 95%	3	86	82	71
	5	94	97	95
	24	100	100	100

2.d) Light

Various authors have attached different significance to light conditions during fructification with regard to subsequent germination of the uredospores. According to Becker (1928) and Wilhelm (1931) a direct exposure to light is said to accelerate the "germination maturity*" of the uredospores and therewith increase the germination capacity.

According to Straib (1940) not only the germination rate but also the maximum germination temperature of the stripe rust uredospores is reduced in the event that the test plants are darkened with starting pustule formation.

I made germination tests with spores (stripe rust race 26) of test plants in order to check these data; these plants were kept under the same conditions of cultivation (diffused daylight, room temperature 15° C) until shortly before the burst of the pustule. With the opening of the first uredostocks some of these plants were covered with dark glass shields (paper lining) for three days, the control plants remaining under the bright glass shields.

The results of these tests are summarized in Table 16. They agree with the findings of Straib inasmuch as the germination rate and the maximum germination temperature of the spores formed in diffused daylight were clearly higher than with the uredospores formed in the dark.

Considerable differences in the germination reaction of a race were mainly found among uredo generations which had been cultivated in the greenhouse in different seasons of the year.

Propagation and germination tests in spring and summer periods of 1961, 1962, 1963 and during the fall and winter months between these periods showed repeatedly that the uredospores formed during the bright time of the year (April until September) germinated much faster and more completely (with differences among the races) than those formed in fall and winter. Usually, the germination depression was particularly great during the shorter daylight months (November until February). Since the races were always propagated at approximately constant temperature and air humidity, the differences

*The term "germination maturity" which was also used by Schaffnit (1909) is not very accurate and cannot be determined since the germination capacity of the uredospores depends on different factors.

in the germination reaction can probably be explained, at least in part, by the differences in light conditions during the various seasons of the year in the period of fructification, since the germination rate and, to a certain extent, also the final germination values developed approximately parallel to the rise and drop of the daily growth length in the course of the year, as Becker had found in 1928. However, I have repeatedly found exceptions to this rule. In these cases it is necessary to take into account factors which have a stronger effect. I will come to this in more detail in Paragraph B. 6.

Table 16

Effect of Light Conditions during the Last Stage of Fructification on Subsequent Germination (in %) of Uredospores of Stripe Rust Race 26 (Substrate 1 % Water Agar)

Light conditions	Germination Temperature (°C)	Germination after Hours		
		3	5	24
darkened	10°	22	65	100
diffused daylight		91	98	100
darkened	20°	-	0	2
diffused daylight		-	19	68
darkened	22°	-	-	0
diffused daylight		-	-	39

B. 3. The Direct Effect of Environmental Conditions on the Germination

3.a) Light

In literature different, partly even contradictory, data are given concerning the effect of light on the germination of uredospores of stripe rust. Eriksson and Henning (1896) were not able to observe any differences in the development of the germination process between germ specimens on water exposed to light and such specimens not exposed to light. Also Wilhelm (1931) who, contrary to Eriksson and Henning, operated with specific stripe rust races and used solid water agar as a substrate, made statements in the same tenor. On the other hand, Stroede (1933) found that at germination temperatures between 11 and 17° C the germination rate was clearly higher within the first six hours in darkness than under exposure to light (daylight or artificial illumination). The results obtained by Straib (1940) contradict Stroede's findings; Straib found that at germination temperatures above 13° C the germination rate of

light-exposed stripe rust spores was clearly higher than that of uredospores germinating in the dark, and that some races germinated much more in light. Only in the case of race 20 which distinguished itself from all other stripe rust races by a very wide germination temperature optimum range and high germination rate, and, in general, with low temperatures (10° C and below), Straib did not find any differences in the development of germination between light-exposed and covered series. Recently, McCracken and Burleigh (1962) have also found that the germination of both fresh and preserved uredospores of P. striiformis was clearly encouraged by exposure to light. The stimulation of the germ by light was found only at a slightly higher germination temperature (> 13.5° C) in agreement with Straib's data, whereas at lower temperatures no difference was noticed between the germination of darkened and light-exposed series.

I have again conducted tests with various stripe rust races in order to clarify these partly contradictory data. As a germination medium I selected 1 % water agar (Merck) in Petri dishes which were set up in greenhouses with approximately constant temperature (15° ± 1° C) -- (on the northern side only diffused daylight). The light intensity closes above the germination dishes fluctuated during the first 5 -- 6 hours after start of the test, between 2200 and 5000 Lux. The dark-exposed series were directly at the side of them.

The test results listed in Table 17 show that the spores completed the germination much faster and also better in terms of percentage when they were not darkened.

Table 17

Effect of Light on Germination (in %) of Uredospores
of Various Stripe Rust Races (Substrate 1 % Water Agar;
Germination Temperature 14 -- 16° C)

Race	Exposure of the Germination Dishes to Light	Germination after Hours		
		3	5	24
20A (T)	Diffused daylight	71	82	93
	Darkness	35	43	46
55 (D)	Diffused daylight	19	30	84
	Darkness	2	4	75
26	Diffused daylight	20	81	-
	Darkness	14	29	-
54	Diffused daylight	-	84	-
	Darkness	-	37	-

Thus, my results agree to a great extent with the experiences gained by Straib, McCracken, and Burleigh. However, I was not able to confirm the statement by Straib according to which race 20 germinated in darkness at the same rate as in light. But the difference in the reaction of various origins of this race has been often observed by me so that a comparison with the race 20 tested by Straib is very questionable.

Let us examine the literature references indicated at the beginning (Eriksson and Henning, Wilhelm): the diverging results of Eriksson and Henning as well as Wilhelm may possibly be explained by the fact that these authors conducted their research only at low temperatures where no differences can be ascertained in the germination reaction between light-exposed and dark-exposed spores.

The data given by Stroede with regard to the effect of light on the germination rate cannot be considered reliable because the temperatures fluctuated to a considerable extent during his tests.

3.b) Temperature

Previous research concerning the effect of temperature on the germination of uredospores of P. striiformis (for example, Eriksson and Henning, 1896; Schaffnit, 1909; Menta, 1923) was conducted without a knowledge of physiological specialization. However, most of the older authors had recognized that stripe rust, unlike other grain rust species (compare Stock, 1931), prefers generally lower temperatures for the germination. Straib found for the first time in 1937 that individual stripe rust races have specific temperature needs.

Table 18 lists the main points of germination temperature of uredospores of P. striiformis as indicated by the various authors.

Since not only pathogenically different stripe rust races but also biotypes partially identical as to pathogenity show different temperature claims in the germination, according to Straib (1939a), I should again examine the germination of various races and origins at different temperatures.

The statement made in Paragraph II is applicable to the cultivation of spores. The spores formed at approximately 15° C. The substrate was only water agar (1 %, Merck); the germ specimens were used always in closed Petri dishes in darkness and exposed to light for a short time only during the ascertainment of the germ numbers. Since no series thermostats but only a few individual thermostats were available, it was

only possible to apply simultaneously a few temperature ranges for the experiments. For technical reasons it was only possible to test a limited number of races simultaneously.

Table 18

Literature References Concerning the Main Point of Germination Temperatures (in °C) of the Uredospores of P. striiformis (Forms Originating from Grain)

Author	Temperature Minimum	Temperature Optimum	Temperature Maximum	Remarks
Mehta, 1923	2--3	?	29	no definite races used
Wilhelm, 1931	(< 5)*	10--20	25	no differences found in the reaction of races during germination
Stroede, 1933	> 0	11--12.5	25--26	
Newton and Johnson, 1936	(< 2)*	10--12	22--25	
Straib, 1940	< 2	9--11 partly 15	23--25 partly 28 or 29.6	differences in reaction of individual races
Manners, 1950	(< 5)*	10--13	22.5--25	--

*No accurate data are available where parentheses are entered.

In the ascertainment of the main temperatures I took into account exclusively the germ percentages but not the rate of germ tube growth and not the final lengths of the germ tubes either. I considered the temperature optimum for the

germination of a race to be that interval where the uredospores achieved full germination or their highest germination percentage within a very short time.

In the majority of tested stripe rust races I ascertained a temperature of approximately 10°C (9° -- 12°C) as the optimal germination temperature on 1 % water agar, regardless of whether fast or relatively slow germinating races were concerned (compare Figure 5).

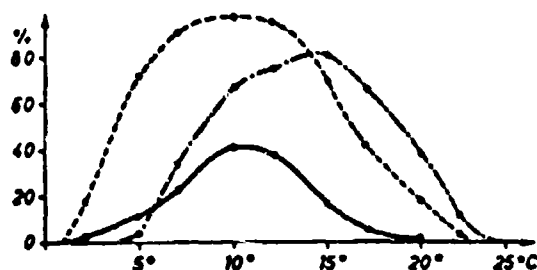


Figure 5. Effect of temperature on germination of uredospores of a few stripe rust races (substrate 1 % water agar (Merck); germination percentages after 4 hours respectively).

———— = race 2 A
 - - - - - = race 7 (Is)
 - . - . - = race 20 A (T)

Stroede, Straib, and Manners (see Table 18) found approximately the same values as optimum temperature with the stripe rust races tested by them on water agar. But Straib also found a few stripe rust races the germination temperature optimum of which was clearly higher than that of most other races. I was able to confirm this inasmuch as the races tested by me 20 A (T) and 20 A (Gr) had a higher temperature optimum (at 15°C) (compare Figure 5).

I was not able to find the strikingly wide optimum which Straib has ascertained for the origins of race 20 used by him.

I found the minimum germination temperature to be approximately 1°C with almost all races. Only the origins (T) and (Gr) of race 20 A germinated already at 5°C only still in

spores (approximately 3%), whereas other races, for example, races 7, 23, 24, 26, and 54 still showed a germination of 70 -- 80% at 2° C after 24 hours.

The temperature maximum fluctuated, depending upon the race, under the selected test conditions, between 20 and 26° C, as can be seen from the list in Table 19.

Table 19

Germination (in %) of Uredospores of Wheat Stripe Rust
Races at Different Temperatures (Substrate 1 % Water Agar)

Race	Germination at				
	10° C		20° C	24° C	26° C
	6 hrs.	24 hrs.	24 hrs.	24 hrs.	24 hrs.
1	22	41	2	0	0
2 A	10	13	0	0	0
7 (F)	96	100	72	3	0
7 (Is)	94	100	70	4	0
8 (D)	37	65	2	0	0
9 (Ke)	95	100	71	2	0
20 A (D)	16	19	3	0	0
20 A (T)	67	93	49	5	0
26	98	100	74	12	2
27/53	92	98	60	2	0
32 A (Sz)	21	33	1	0	0
42 A	65	78	35	1	0
54 (D)	84	96	56	1	0
55 (F)	70	90	14	0	0
55 (Sz)	11	15	0	0	0

The results listed in this table originated from a test series in which parallel propagated wheat stripe rust races had been tested under the same cultivation and fructification conditions simultaneously. With several repetitions with other uredospore generations of the same race, in principle, the same germination reaction was observed.

It was always found that the races germinating relatively quickly and fully (for instance, 7, 9, 26 and others) at medium temperature of germination (8 -- 15° C) showed the highest germination percentages at higher temperatures which approached the maximum; they also had the highest germination temperature maximum as had been found previously by Straib (1940) and Manners (1950). Race 26 (origin: Holland) showed the highest temperature maximum.

With the stripe rust races and origins germinating slowly and to a smaller extent (for example 1, 2 A, 8 (D), 20 A (D), and others) only a very slight germination or no germination at all was obtained already at 20° C, whereas the relatively fast germinating races still showed a slight germination at 24° C or even 26° C.

A comparison of the development of germination of the barley stripe rust races 23 and 24 showed that the greater germination rate of race 23 parallels a higher temperature maximum (Table 20).

Table 20

Germination (in %) of Uredospores of the Barley Stripe Rust Races 23 and 24 at Different Temperatures (Substrate 1 % Water Agar)

Race	Germination at					
	10° C		17° C	20° C		24° C
	3 hrs.	24 hrs.	24 hrs.	6 hrs.	24 hrs.	24 hrs.
23	70	100	81	25	41	3
24	38	97	14	2	3	0

It must now be expressly pointed out that the temperature maximum for the germination of a race cannot be accurately established; it differs depending upon the fructification conditions (compare Paragraph B. 2.b)) and the germination substrate. I have pointed out above that the stripe rust races germinated much more if slightly acidified agar substrates (pH 4.5) were used instead of pure water agar (pH 6.2). Also small additions of primary Na-, K- or particularly ammonium phosphate ($\text{NH}_4\text{H}_2\text{PO}_4$, 0.01 -- 0.005 mole), the favorable effect of which on the germination of stripe rust uredospores had been recognized by Wilhelm (1931) and Straib (1940), increased the temperature maximum by 2 -- 3° C. I was able to confirm this in the germ test with races 1, 7, 9, 23, 24, 26 and others to the fullest extent.

Special mention must be made of the differences in the germination reaction of pathogenically identical biotypes of race 20 A depending upon the temperature. In Paragraph A. 2 I referred to the different germ tube growth types within this group. Repeatedly conducted germ tests of the biotypes 20 A (D) and 20 A (T) now resulted in secured differences with regard to germination at different temperatures (germination rate, temperature maximum and final germination values) as can be seen from the average results (computed from numerous individual values) listed in Table 21.

Table 21

Germination (in %) of the Uredospores of Two Origins (Biotypes) of the Stripe Rust Race 20 A at Different Temperatures (Substrate 1 % Water Agar)

Biotype	Germination at				
	10°C		20°C		22°C
	6 hrs.	24 hrs.	6 hrs.	24 hrs.	24 hrs.
20 A (D)	16.0 (+5.0)	30.0 (+17.0)	3.0 (+1.3)	5.6 (+2.5)	0
20 A (T)	71.0 (+7.2)	83.5 (+14.5)	37.0 (+4.8)	48.4 (+8.8)	40.0 (+0)

A biotype coming from Greece, race 20 A, showed the same germination reaction under all temperature conditions as the type from Turkey. The growth pattern of the germ tubes was also the same with these two biotypes.

Striking differences in the germination reaction and temperature dependency were found between two biotypes of the wheat stripe rust race 55, which were always confirmed in repeated tests of various uredospore generations: the French type germinates always relatively fast and at approximately 10 -- 15° C completely in most instances, whereas the Swiss biotype germinated extremely slowly and to a very small extent; with this origin the temperature maximum was always approximately 3° C lower than with the French biotypes.

B. 4. The Fructification Period as a Characteristic Feature of Individual Stripe Rust Races

Naturally, the fructification period of stripe rust is greatly influenced by environmental factors, particularly the temperature and illumination. As soon as these factors drop below the optimum, the start of sporulation is delayed accordingly. This relationship is shown particularly clearly with the comparison of the fructification times between summer and winter cultivations. According to Manners (1950), for example, the fructification time with *P. striiformis* is only 10 -- 12 days in summer, but 13 -- 18 days in winter. In view of the dependency of merely the germination rate alone upon various environmental factors, described above, this cannot surprise us.

I have observed similar fructification times as indicated by Manners, with the continuous propagation of stripe rust races on wheat and barley germ plants at an average greenhouse temperature of 15° C. In addition, I was able to ascertain that clear differences resulted in the fructification time of individual stripe rust races, in spite of a simultaneous inoculation and parallel cultivation under the same environmental conditions: some races, for instance, during the summer months sporulated after only 10 days; others started to fructify only after 12 days. During the season with poor light, the fructification time was longer by an average of 2 -- 3 days. The relative differences between the races, however, remained in all seasons, regardless of the species of host, provided that they were highly susceptible species. Therefore, we can classify some races as relatively fast fructifying races (for example, 7 (Is), 26 and others) and others as slowly fructifying races (for example, 2 A, 55 (Sz)).

It must be pointed out that a clear relationship exists between the fructification time of one race and its germination reaction. Those stripe rust races which germinated fast had high germination numbers and a higher temperature maximum, were also characterized by a shorter fructification time than the races which germinated slowly and had a lower temperature maximum.

I have reproduced the values observed with races 2 A and 7 (Is) in Figure 6.

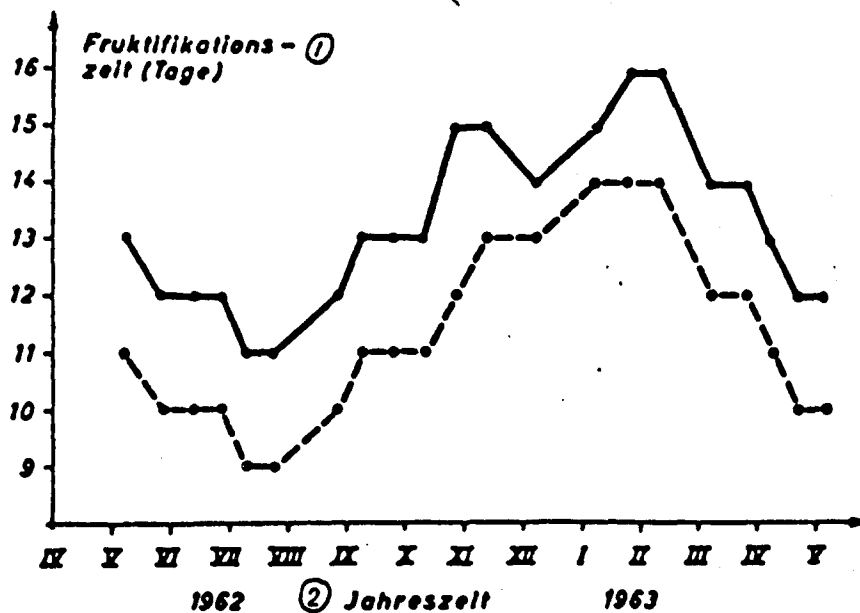


Figure 6. Fructification time as a function of the season with two wheat stripe rust races after simultaneous inoculation on Triticum dicoccum tricoccum (cultivation temperature approximately 15° C).

• — • = race 2 A

o - - - o = race 7 (Is)

1 -- Fructification time (days);

2 -- Season.

B. 5. Investigations on the Self-Inhibition of Germinating Stripe Rust Uredospores

In the physiological investigations of uredospores of different species of rust, attention was repeatedly drawn to a phenomenon which had been called "self-inhibition" by Allen (1955) and was in agreement, to a great extent, with similar experiences gained previously with other microorganisms (Literature: see Cochrane, 1958, pages 413 -- 415; and Table 22). This self-inhibition was observed by the fact that the spores completed the germination less with closer distribution. If spores were suspended in water in large quantities, an inhibiting effect was noticed if fresh spores were sown on the filtrate of the spore suspension, the inhibiting effect decreasing with a dilution of the washing water used for the spores.

Table 22

Literature References Concerning the Self-Inhibition
of the Uredospores Germination of Different Rust Species

Author	Species of Rust
Yarwood, 1954	<i>U. phaseoli</i>
Allen, 1955	<i>P. graminis tritici</i>
Forsyth, 1955	<i>P. graminis tritici</i>
Yarwood, 1956 a	<i>U. phaseoli</i>
Yarwood, 1956 b	<i>U. phaseoli</i>
	<i>P. helianthi</i>
Le Roux and Dickson, 1957	<i>P. sorghi</i>
Wilson, 1958	<i>P. carthagen.</i>
	<i>P. graminis tritici</i>
	<i>P. helianthi</i>
	<i>P. polygoni amphibii</i>
	<i>U. phaseoli</i>
Naito et al., 1959	<i>P. coronata</i>
Talieva, 1961	<i>P. suaveolens</i>
Bell and Daly, 1962	<i>U. phaseoli</i>
Hoyer, 1962 a	<i>P. recondita tritici</i>
	<i>P. antirrhini</i>
	<i>P. recondita scabris</i>
	<i>P. sorghi</i>
	<i>U. fabae</i>

Therefore, the cause of the germ inhibition was explained by a principle of matter ("inhibitor") which diffused from the spores into the germination medium. However, it was not possible to ascertain the chemical composition of the inhibiting agent so far. It is true Forsyth (1955) believed to have found trimethylethylene with *P. graminis tritici* and Wilson (1958) thought he had found aspartic and glutamic acid with *U. phaseoli* as "self-inhibitor" substances, but it was not possible to furnish safe evidence of the identity of the inhibiting substances with the mentioned compounds.

Since no experience was available whether a self-inhibition develops with P. striiformis in the uredospores, I have examined several stripe rust races in this regard.

Preliminary tests

A self-inhibiting effect was established in preliminary tests with uredospores of the barley stripe rust race 24 with two methods:

1. The germination percentages drop to a great extent on agar substrates or distilled water with increasing spore density (however, it was not possible to ascertain the germination numbers in an accurate manner with the high seeding density).

2. If spores were suspended for several hours in distilled water (approximately 0.1 g/10 ml) at different temperatures (5 -- 20° C) and if, subsequently, fresh spores were put on through a normally distributed thin seeding (< 1 mg spores/3 ml in germ dishes of a diameter of 5 cm) on the filtered spore cleansing water, then their germination was greatly reduced compared to the controls.

Material and method

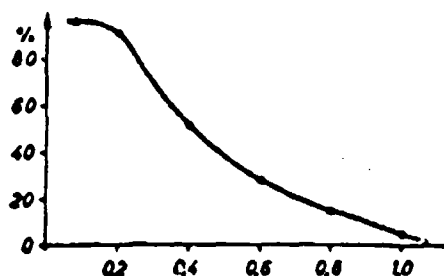
In the main experiments I used spores of the stripe rust race 24 formed outdoors, and wheat stripe rust races 8 (D) and 54 (compare also Paragraph II). The freshly harvested spores were suspended in 200 ml Erlonmeyer flasks at the ratio of 1:100 (0.5 g of spores/50 ml) in distilled water; the flasks were closed with a cotton stopper and left standing in the cooling cabinet for 24 hours and a temperature of +5° C. Subsequently, the spore suspension was filtered through a glass frit (G 3). Unless prescribed otherwise, the filtrates of the spore washing water were mixed at equal parts with a 1 % water agar and 3 ml of it each were poured into Petri dishes (diameter 5 cm). The germination dishes were set up at 10° C in the dark thermostat. As a control substance I used 0.5 % water agar. After 24 hours I ascertained the germination in percentages.

5.a) Investigations concerning the germination inhibiting effect of aqueous spore diffusates

Following the filtrates of the spore washing water are designated by the numbers of the races from whose spores the diffusates had been obtained.

Filtered washing water of uredospores of race 24 proved to be greatly germination inhibiting for untreated and

previously washed spores of the same race. Whereas the spores on the controls germinated to the extent of 80 -- 95 %, a germination of only approximately 1 -- 5 % was obtained on the agar substrates containing spore washing water. When the spore diffusate was diluted stepwise, the germination inhibition decreased progressively (Figure 7).



Relative concentration
of inhibiting substance

Figure 7. Germination of Uredospores of Stripe Rust Race 24 on Spore Washing Water (24) at Various Concentrations (Germination at 10° after 24 hours)

The filtrates of the spore washing water of race 8 (D) also inhibited untreated and washed spores of their own race to a great extent; here again, the extent of germination inhibition was always dependent upon the concentration of the spore diffusate. The spore diffusates of races 8 (D) and 24 did not only inhibit the germination of spores of its own, but, in both cases, also that of the other stripe rust race. If, on the other hand, spores of race 7 (Is) were put on the spore washing waters 8 (D) and 24 for germination, then they were not inhibited or only to a small extent; I was able to ascertain this in the same manner in five different tests which I had repeated.

I was able to observe this difference in the inhibiting effect to a great extent with tests of different diffusates and races which I had repeated several times. Diffusate 24 inhibited, for example, the germination not only of race 8 (D) to a great extent, but also the germination of 20 A (D); it

prevented almost completely the germination of the barley stripe rust races 23 and 24. Not inhibited were 8 (Is) and 7 (F), 9 (Ke), 26 and 54, as mentioned before.

Diffusate 54 also inhibited 8 (D) and 20 A (D); it did not inhibit 7 (Is), 7 (F), 9 (Ke), 26 and, surprisingly, it did not inhibit the spores of the same race 54, and only to a very small extent the spores of the stripe rust races 23 and 24.

These tests show that the effect of the inhibiting substance and the tolerance of the various stripe rust races \pm seem to be specific.

In further tests I examined the effect of spore diffusates 8 (D), 24 and 54 with regard to the germination of freshly harvested uredospores of different races of P. recondita tritici. In all cases these diffusates did not inhibit the germination of the wheat brown rust races at all, which completed germination after only 3 hours in the same way as on the control substrates (0.5 % water agar) to the extent of 95%.

5.b) Investigations on the nature of the inhibiting agent

The following investigations were exclusively made with spores of the barley stripe rust race 24 and the spore diffusates ("solutions of inhibiting substance") of this race.

The filtrates obtained after separation of the spores were colorless or dyed slightly yellow. Sometimes, but not with all cultures, an odor similar to fruit ester* emanated from the solutions.

The filtrates had a pH of 6.0 -- 6.3 (pH of the distilled water used for the spore suspension: 5.5). Since these pH values had proven to be optimal for the germination of the stripe rust uredospores previously, and pure water agar, which was used as a control substrate, did not show an essentially different acidity (pH 6.1), I conducted all experiments with uncorrected pH and non-buffered inhibiting solutions.

*The same phenomenon was observed by Schaffnit (1909) after a storage of large quantities of spores of different species of grain for one day in closed receptacles, and particularly after adding water, and described as a "wonderful blossom odor."

Solubility in Ether

The greatly germination-inhibiting aqueous spore diffusate was intensively shaken with pure diethylether at the ratio of 1:2 (Volume T.). Subsequently, the ether was evaporated at room temperature and the small ether residue was resolved to the initial volume of the spore diffusate.

The subsequent germination tests showed that the inhibiting agent had been transferred to a great extent from the aqueous phase to the ether:

<u>Germination Test at 10° C on:</u>	<u>Germination Percentages after 24 Hours:</u>
Spore diffusate, untreated.....	2
Spore diffusate, shaken with ether	70
Ether residue of spore diffusate resolved in distilled water.....	15
Distilled water (control).....	92

Adsorption

It was possible to adsorb the inhibiting agent almost completely by adding powdered activated carbon to the spore washing water filtrate, but not by silica gel (silica gel G for chromatography):

<u>Germination Test at 10° C on:</u>	<u>Germination Percentages after 24 Hours:</u>
Spore diffusate, untreated.....	2
Spore diffusate, treated with activated carbon.....	87
Spore diffusate, treated with silica gel.....	4
Distilled water (control).....	90

Heat Resistance

Various specimens of the spore diffusate were put into glass ampoules which were closed and heated for 60 minutes,

respectively, in boiling water bath and an autoclave at 120°/1 atmosphere gauge. Further specimens were kept boiling in a boiling flask with a reflux condenser put on for 60 minutes. Subsequent germination tests on the treated solutions showed that the inhibiting agent was in no case destroyed by the heat. The germination was only 2 -- 5 % on the previously heated solutions and the untreated spore diffusates, as against 92 % on the control dishes with distilled water.

Volatility

It was not possible to examine a volatility of the inhibiting agent at room temperature, as found by Allen (1955) and Forsyth (1955) with P. graminis tritici, as well as Hoyer (1962b) with P. recondita tritici by corresponding germination tests, in tests with stripe rust spores and the washing waters obtained from them, since the temperature around 20° C greatly inhibited the germination of the stripe rust spores which were used here.

In tests made at more favorable germination temperatures (10 -- 15° C) the stripe rust spores germinated on agar plates exposed, at a distance of 5 mm, in closed germination dishes for 24 hours, to stripe rust spore diffusates containing inhibiting substances, at a rate of approximately 90 %, in the same way as the controls. This showed that the inhibiting agent of the spore diffusates was not volatile at low temperatures or not in effective quantities.

On the other hand, the inhibiting agent proved water vapor volatile in the distillation of aqueous spore diffusates. Forty ml of a spore washing water filtrate were distilled over in an apparatus with ground joints (Jena glass) at 100° C in ice-cooled receivers; approximately 10 ml of the distillate were collected separately at a time, successively. The very small residue, the appearance of which was similar to that of oil, was subsequently dissolved again in 40 ml of distilled water.

I mixed the various fractions with equal parts of 1 % water agar and examined for their activity. The germination tests which were repeated twice with spore diffusates prepared with further distillate specimens, showed in all cases that the inhibiting agent is volatile with water vapor. In the specimens prepared with the distillates and resolved residue, the germination was 4 -- 7 % as against 82 % on the controls. It was confirmed again that it is not impaired with regard to its effect by the distillation or impact of the heat. Since also the residue of the distillate inhibited the germination to a great extent, it is assumed that there are at least two

compounds in the spore washing water which have an inhibiting effect unless an inhibiting substance is divided into a non-volatile one and a substance which is volatile with water vapor, through the heating process, both having a germination inhibiting effect.

The effect of aspartic and glutamic acid on the germination of uredospores

Wilson (1958) was able to establish with the chromatographic method aspartic and glutamic acid in germination inhibiting aqueous uredospore diffusates of U. phaseoli. Since these amino acids inhibited the germination of the bean rust spores in vitro to a greater or lesser extent, in certain concentrations, Wilson made these compounds responsible for the self-inhibition of germinating spores. Bell and Daly (1962) as well as Hoyer (1962b), however, believed that they could establish that the germination inhibition of uredospores of U. phaseoli and P. recondita tritici effected by higher concentrations of aspartic or glutamic acid was based only on an unspecific acid effect (unfavorable change of the pH of the substrate). Since relatively high concentrations of these acids did not suppress the germination when the amino acids had been neutralized, these authors excluded aspartic and glutamic acids as self-inhibiting substances of the mentioned rust species.

I have found in repeatedly applied tests that also the germination of stripe rust uredospores of different races [7 (Is), 23, 24, 26] was not inhibited even by 1000 ppm of aspartic or glutamic acid (single or in a mixture) with the buffering of the substrate (pH 5 -- 5.5) or the neutralization of the amino acids by n/10 NaOH. Thus, both acids cannot be considered self-inhibiting agents of germinating stripe rust uredospores, as far as they have been examined.

Effect of 2.4 dinitrophenol (DNP) and coumarin on the germination of uredospores

Farkas and Ledingham (1959) observed on "self-inhibiting" uredospores of P. graminis that in the presence of DNP (10^{-5} M), coumarin ($5 \cdot 10^{-4}$ M) or particularly pelargonaldehyde ($5 \cdot 10^{-4}$ M), consumption of O_2 rose sharply during the first hours and the germination was stimulated considerably. Since additions of propionate and butyrate in non-catalytic volume did not influence the self-inhibition in the same manner, the authors concluded that the use of endogenous fatty acids is blocked by the self-inhibition.

Also Allen (1955) proved that DNP and cumarin eliminate the germination inhibition to a great extent, in certain concentrations, with the "self-inhibited" black rust uredospores. Finally, Hoyer (1962b) was able to observe that the self-inhibiting effect with P. recondita tritici could be eliminated by DNP and cumarin. In the concentration range in which DNP or cumarin encouraged the germination of not-inhibited uredospores, the effect was compensated by spore cleansing water containing inhibiting substance; with a constant concentration of inhibiting substance the germination decreased until it was eliminated completely*, with an increasing concentration of DNP or cumarin in the range of $5 \cdot 10^{-7}$ to $5 \cdot 10^{-4}$ M (for DNP) and 10^{-5} to $5 \cdot 10^{-3}$ M (for cumarin).

The method indicated by Hoyer (1962b) was used in order to check whether the inhibiting effect of the spore diffusates can be eliminated or diminished also with stripe rust spores by DNP or cumarin. However, the results of these tests were negative. DNP and cumarin which were added to the washing water at different concentrations ($5 \cdot 10^{-3}$ - 10^{-7} M) either immediately with the spore suspension or only after filtering the spores did not diminish the effect of the spore diffusates. On the control substrates (without spore washing water) concentrations from 10^{-4} M of DNP on, and from $5 \cdot 10^{-3}$ M of cumarin on, resulted in a complete germination inhibition whereas 10^{-5} M of both substances did not impair germination.

If we again summarize the properties of the inhibiting agent recognized so far, differences appear in various respects compared to the inhibiting substances observed in other rust species:

1. Under long heating of its aqueous solution the "inhibiting substance" of the stripe rust spores proved heat resistant. This agrees with the statements by Allen (1955). On the other hand, Hoyer (1962b) found that the inhibiting effect of wheat brown rust spore diffusates was greatly eliminated with the same treatment.

2. Whereas the stripe rust spore diffusates had a germination inhibiting effect also after their distillation, this did

*On the other hand, higher concentrations of both compounds completely inhibit the germination of the brown rust spores also on the control substrate.

not apply to the spore diffusates of P. recondita tritici (Hoyer, 1962b). In the same manner, Allen (1957), French et al. (1957) observed that the distillation of aqueous uredospore extracts of P. graminis tritici led to an inactivation of the inhibiting substance.

3. The distillates of the stripe rust spore diffusates also showed in different dilutions merely a correspondingly weaker germination inhibiting effect; they did not exert a stimulating effect nor did they encourage the formation of vesicles of germinating uredospores as Allen (1957), French et al. (1957) had found with distillates of black rust uredospore diffusates.

4. It was not possible to eliminate or diminish the effect of the inhibiting substance of P. striiformis by adding certain quantities of DNP or cumarin, whereas the self-inhibition of the spores of P. graminis tritici (Allen, 1955; Farkas and Ledingham, 1959) and of P. recondita tritici (Hoyer, 1962b) was compensated by certain concentrations of these compounds to a greater or lesser extent.

On the other hand, the inhibiting agent of the stripe rust spores also showed some of the same physical properties as the inhibiting substances of other rust species. Bell, Daly (1962) and partly also Hoyer (1962b) found an ether solubility, adsorption of the "inhibitor" on activated carbon and non-adsorption on silica gel, with the inhibiting substances of the spores of U. phaseoli and P. recondita tritici. However, these properties are not very specific and do not permit any conclusions as to the chemical nature of the inhibiting agent.

B. 6. Relationship between the Development of Weather Conditions and the Germination of Uredospores

In the above paragraphs I have confirmed and amplified the statements made by other authors according to which the germination of uredospores of stripe rust is influenced by numerous factors indirectly and directly, the details of which are known to us and can be controlled to the optimum extent possible within certain limits. In particular, these factors include temperature, light, humidity and the germination substrate. Further tests showed that the germination of the uredospores depends to a greater or lesser extent on the presence of so-called "self-inhibiting" substances formed by the rust spores.

Although I maintained to a great extent constant conditions under the tests over months in repeatedly applied experiments with artificial substrates, surprising fluctuations were found

in the germination process from time to time which were ascertained in parallel preparations of different spore origins (races) in the same manner and could not be directly explained by any changes of the above-mentioned environmental factors. These observations gave rise to the question whether the germination of stripe rust spores is also influenced by factors which had not been taken into account up to the present time; this would mainly apply to "factors of weather."

In earlier literature reference was made to the presumed impact of weather on the germination of fungus spores in various instances (Fischer and Gäumann, 1929, page 243). However, a more exact knowledge of the meteorobiological relationship, particularly with microorganisms, was provided by subsequent investigations by Bortels (for literature see Bortels, 1959). In continued series tests with Azotobacter chroococcum Bortels found that the nitrogen compound and the propagation of this bacterium was usually greater under rising than falling air pressure. Also with other objects Bortels found a very similar parallelism between certain manifestations of life and the development of the weather: with an anticyclonic development of the weather (rising pressure) more zoospores were active, for example, with Phytophthora infestans sporangia and one type of yeast copulated more in anticyclonic weather than under falling pressures. The fact that aerobic (oxidative) reactions were concerned was a factor which these and other microbiological processes had in common in the tests Bortels had conducted.

Anaerobic processes were influenced by the same development of weather in the opposite direction: reductions and fermentation processes were more intensive under a cyclonic development of the weather than under an anticyclonic one (Bortels, 1950).

In addition, Bortels and partly also other authors established that also inactivated physical and chemical systems may be influenced in different ways by an unknown weather agent depending on the cyclonic or anticyclonic development of the weather (stimulation or retardation of the syneresis of colloidal systems, for example, water agar and serum under falling and rising air pressure, respectively, etc.).

In numerous tests with different organisms and the above-mentioned physical and chemical reactions various authors found that these phenomena referring to the weather may be modified or superimposed by solar activity. Accordingly, the relationship of microbiological and other reactions appear to be most pronounced with decreasing or negligible activities of spots and less pronounced with a quick increase or at the maximum of solar spot activity.

In many cases Bortels established that the effect of the unknown weather factors made itself felt shortly before cyclonic or anticyclonic changes of weather. This showed that the air pressure proper could not be made responsible for meteorological developments.

On the basis of further experiments where the effect of the weather agent on activated and inactivated objects of investigation was partly shielded by screening or mere covering with various metals (here again it was necessary to take into account the solar activity) Bortels (1950) came to the conclusion that the unknown weather agent can be explained by a radiation which seems to be of solar origin, at least to a great extent.

The weather radiation theory of Bortels states that with a cyclonic development of the weather, relatively soft "T rays" appear which encourage, for example, reductions, anaerobic fermentation and aggregations. On the other hand, with an anticyclonic development of the weather hard "H rays" are acting which encourage oxidation, aerobic respiration and their resultant phenomena (generative propagation, yield of crop). "Thus, the development of the weather and biological reactions are not related to each other as is a cause to the effect, but both are more or less parallel phenomena, the effect of a cause (radiation) they have in common, or of a complex group of rays" (Bortels, 1951).

The following description is based on observations I made in certain germination tests with stripe rust spores from December 1961 until spring 1963. For reasons beyond my control, it was not possible to complete the investigations on the relationship between the development of the weather and the germination behavior. The needed spore material was not available through the entire period and the study of other problems was given preference. The tests were made more difficult because the air-conditioned room I used was only available for a short period, otherwise the stripe rust races could have been cultivated parallel to the conventional greenhouse cultures. Therefore, on the basis of these tests I cannot claim to have analyzed this complex problem of stripe rust uredospores in an exhaustive manner.

The following procedure was applied in the tests described below:

The stripe rust races were raised with the usual method in a greenhouse with approximately constant temperature (15° C) in diffuse daylight, during the winter half-year with additional illumination (see Paragraph II). I have propagated the races in the air-conditioned room with the same method under constant

light, temperature and air humidity conditions, parallel to the greenhouse cultures.

Before the infected host plants (Triticum dicoccum tricoccum for wheat stripe rust races, barley of Fong-Tien for the barley stripe rust race 24) started to sporulate, I covered them with light glass shields (relative humidity > 95 % under the shields). I removed the uredospores formed first and then I shook off the spores which had been newly formed within approximately 24 hours, in glass receptacles, mixed them intensively and used them right away for the germination tests.

As germination substrate I used only 1 % water agar (purified agar for nutrient media from Merck). The agar soils were prepared with freshly distilled water for each test, 3 ml each of the non-sterilized agar solutions poured out into Petri dishes (diameter 5 cm) and the spores were sprayed on the substrate, as far as possible evenly and thinly distributed (approximately 0.5 mg per germ dish) -- (3 -- 5 parallels per race with each test). The seeded Petri dishes were then immediately put into the dark, closed, under thermostatic check (germination temperature 10° C); with race 20 A (T) the temperature was 15° C. I ascertained the percentage of germination after 3, 6, and 24 hours.

The first criteria for the action of an unknown weather agent on the germination reaction of stripe rust uredospores were provided by germination tests on agar substrates, which as a control for tests with other problems were prepared always with new spore biotypes from the greenhouse as a routine at intervals of a few days. Whereas the uredospores of these races germinated in November and the first half of December 1961 in an extremely slow and weak manner (after 6 hours < 10%, after 24 -- 48 hours approximately 20 % as a maximum), a test on 14 December 1961 resulted in the surprising fact that the spores had completed germination only after 6 hours to the extent of > 80 % and > 90 %, after 24 hours to the extent of approximately 95 % (compare Figure 8).

The weather showed the following pattern: in the second half of November until 12 December cloudy weather prevailed, influenced throughout by low-pressure areas, at the place of testing. On 11 December 1961 a strong high-pressure zone started to determine the weather after a preceding new fall in pressure (low pressure) -- (lasting steep rise of pressure, connected with dropping outside temperatures, at the beginning with slight snowfall and subsequent clearing up; direction of the wind from southwest to west over northwest turning toward northeast). With this change from cyclonic to a typically anticyclonic weather, a clearly improved germination capacity of

the spores went along, which had been formed during this transfer from low to high pressure. An observation very similar to this was made in January 1963. A sudden improvement in the germination developed during the change from the low pressure to a new high pressure weather after only negligible germination had been observed during the preceding testing days during which continental winter weather had prevailed almost throughout. Two parallel propagated stripe rust races showed exactly the same reaction (Figure 9).

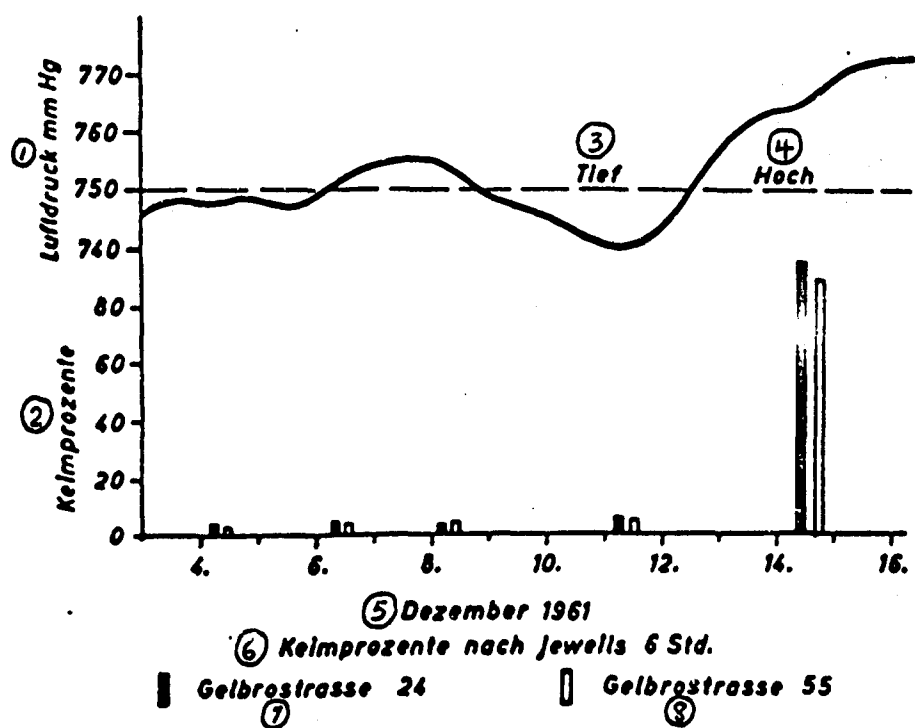


Figure 8. Relationship between the uredospore germination of P. striiformis and the development of the weather (for details see the Text).

1 -- Barometric pressure mm Hg; 2 -- germination percentages; 3 -- low; 4 -- high; 5 -- December 1961; 6 -- germination percentages every 6 hours; 7 -- stripe rust race 24; 8 -- stripe rust race 55.

In 1962 an air-conditioned room was available part of the time in which stripe rust races were propagated parallel to the greenhouse cultures. Since the incubation time in the greenhouse and in the air-conditioned room was the same, it was possible to harvest and test the spores after simultaneous cultivation, at the same time.

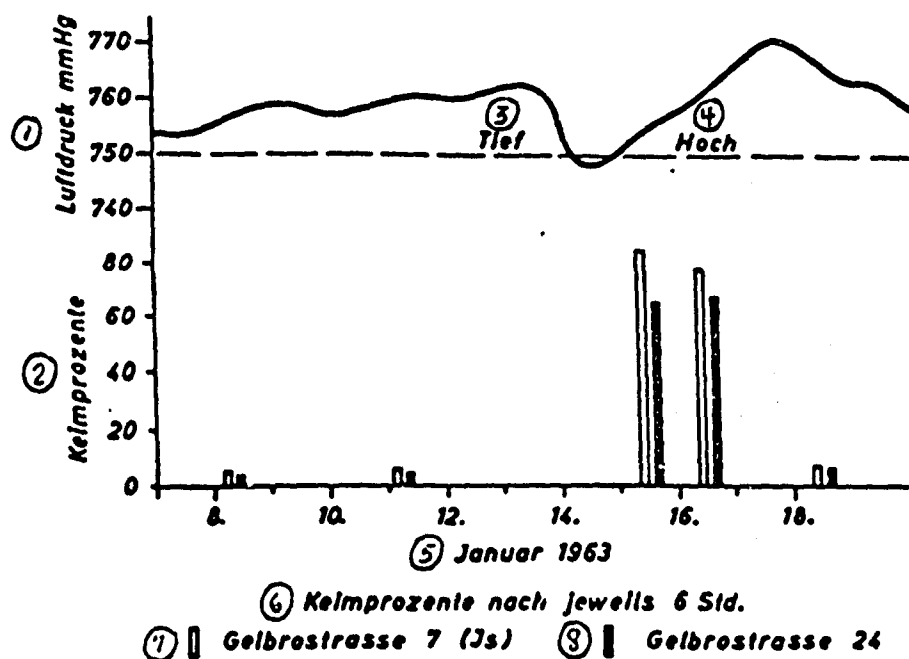


Figure 9. Relationship between the uredospore germination of P. striiformis and the development of the weather (for details see the Text).

1 -- Barometric pressure mm Hg; 2 -- germination percentages; 3 -- low; 4 -- high; 5 -- January 1963; 6 -- germination percentages every 6 hours; 7 -- stripe rust race 7 (Is); 8 -- stripe rust race 24.

Very conclusive was the result of a test series with newly formed spores of two wheat stripe rust races which had been propagated several times from the beginning of May until the beginning of June 1962. The spore origins coming from the greenhouse and the air-conditioned room germinated at a slow rate during the tests made in May, which surprised us. The local weather was dominated throughout the entire month by low-pressure zones or extensions of such zones. At the same time shower-like rain precipitated unusually often. The characteristic singularity of the cold days in May did not appear at the place of testing in that year. Around the 2nd and 3rd of June the weather changed completely; a wide Atlantic high-pressure zone started to prevail with its typical weather criteria (continuing rise of pressure; at first slight cooling off: winds turning from northwest to northeast; subsequently, the weather cleared up).

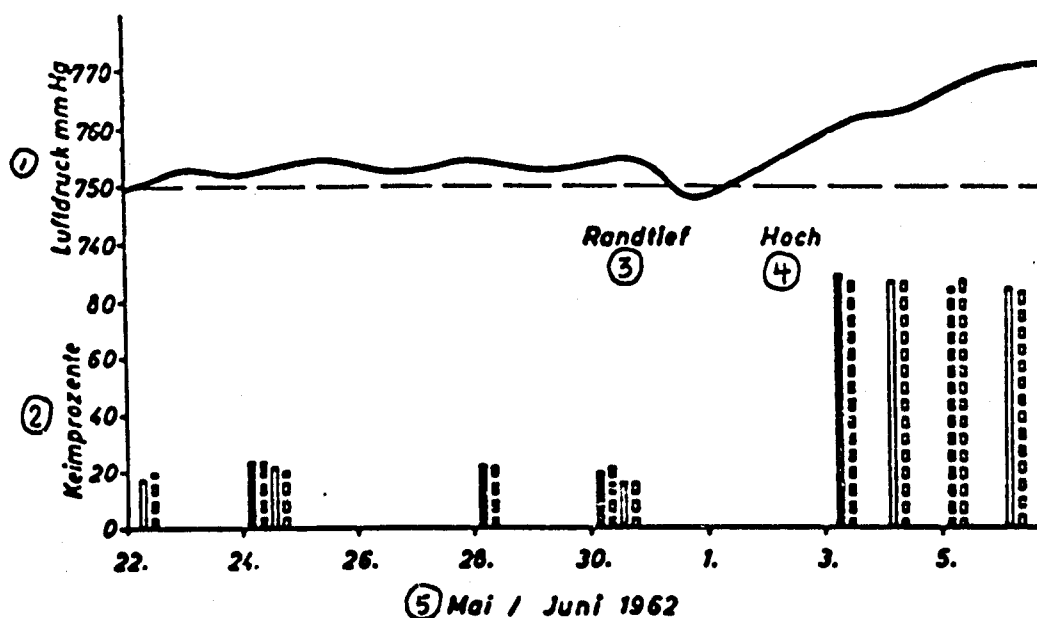
The spores which ripened at that time in the greenhouse and in the air-conditioned room now germinated after only 3 hours to the extent of approximately 80 -- 90 %; after 6 hours a germination of almost 100 % was ascertained with all specimens (the dispersion rate of parallel cultures of one origin was approximately 5 -- 8 %). On the other hand, in the test conducted in May, only approximately 15 -- 25 % of the spores had completed germination, on the average, after the same period of germination of 3 hours (Figure 10). Also with a stripe rust race which had been propagated from May 1962 on outdoors, a remarkably stronger germination was observed at the start of this high-pressure period contrary to the tests repeated in May several times*. Only after 3 hours these uredospores germinated to the extent of more than 80 % and after 24 hours for more than 90 %, whereas in the tests made during the preceding weeks, less than 10 % of the spores had germinated, on the average, after 3 hours, and only about 40 -- 50 % of the spores after 24 hours.

From these observations which were made repeatedly in further tests under similar weather conditions, the conclusion must be drawn that the germination reaction of the stripe rust uredospores can be greatly modified by the agent which Bortels termed "weather radiation," since all other factors which had an effect upon the process of germination were excluded from a possibility that they could be considered a cause of the differences in the reaction, at least in the tests with spore origins from the air-conditioned room. However, with regard to the described tests with spores of greenhouse cultures the same cause must be assumed for the fluctuating germination reaction: For example, the light conditions of the greenhouse were not more favorable at all during the pronounced changes of weather, (December 1961, January 1963) when, all of a sudden, a quick and strong germination was observed, than during the preceding weeks; on the contrary, the daylight was less intensive during this testing period as a result of a snow cover on the greenhouse than before, whereas the temperature and the air humidity of the house remained constant.

At the beginning it was indicated that the change in air pressure and the development of weather conditions connected with it are merely symptoms of the "weather factor" so far not

*Sporulation leaves were cut off from the wheat plant of the field; the spores which had formed at this stage were removed; the leaves were put into humid chambers and the newly formed spores were utilized after 24 hours.

accurately defined, which influence the biological development. The relationship between both parallel phenomena stood out clearly in the few cases investigated here. However, the premises for a statistical evaluation of the tests were not present.



⑥ Keimprozent nach jeweils 3 Std.

- ⑦ | Gelbrostrasse 7 (Js) - Gewächshaus-Anzucht
- ⑧ | " " 7 (Js) - Klimakammer-Anzucht
- ⑨ | " " 20A (T) - Gewächshaus-Anzucht
- ⑩ | " " 20A (T) - Klimakammer-Anzucht

Figure 10. Relationship between the uredospore germination of P. striiformis and the development of the weather (for details see the Text).

1 -- Barometric pressure mm Hg; 2 -- germination percentages; 3 -- secondary depression; 4 -- high; 5 -- May/June 1962; 6 -- germination percentages every 3 hours; 7 -- stripe rust race 7 (Is) -- greenhouse culture; 8 -- stripe rust race 7 (Is) -- air-conditioned chamber; 9 -- stripe rust race 20 A (T) -- greenhouse culture; 10 -- stripe rust race 20 A (T) -- air-conditioned chamber.

In general, it was found, however, that the germination rate and possibly also the final germination values of the yellow uredospores (with differences between the races), with lasting cyclonic weather, are more or less reduced depending upon the season of the year. Whereas with marked anticyclonic weather development in spring and summer, the germination (rate of germination) was clearly accelerated, this did not apply to lasting high-pressure weather in winter (particularly clearly in December 1962 until February 1963). It was also ascertained by Bortels that high-pressure zones have mostly little biological effect in times of a very low position of the sun. This means at the same time that the absolute barometric values are not the decisive factor in the biological effect of the variable nature of the weather. According to Bortels (1951) "the effective agent ... is not found in statistics but in the dynamics of weather development ..."

Apparently, the impulse released by the weather agent in the spores goes through the metabolism of host and parasite and is fixed in the spores. In no case did I observe that the initially found germination reaction (high or low germination force) changed over to an opposite reaction during repeated germ tests with spores stored for a few days if a new change of weather occurred in the meantime.

It remains an open question in which way and whether the "weather factor" in the described tests also has had an effect through the inactivated substrate. But as far as can be deduced from my observations, such an effect is not necessary to be taken into account. No differences were found on the water agar plates which had been prepared partly before and partly during a biologically effective change of weather and subsequently used for the germination tests.

IV. DISCUSSION

The uredospores of stripe rust have an average size of $20.8 \mu \times 17.3 \mu$ (± 1.2) as far as origins from wheat or barley are concerned. In literature we find sometimes deviating statements. Large dimensions as were, for example, indicated by Straib (1941) are explained by the strong and quick swelling of the spores in aqueous media as was observed by Allen (1928); my investigations have established this in a convincing manner.

Whereas no differences were found with regard to the size of the uredospores between the investigated races, it was found that the growth pattern of the germ tubes with the biotypes originating from wheat and barley was clearly different on the basis of certain culture and germination conditions. Straib (1939a) was the first to recognize this characteristic feature

of the two racial groups; however, subsequently, he limited the scope of his statement after he had found a few exceptions from the rule. However, I confirmed the previous data of Straib to the fullest extent which is all the more remarkable as I had operated with races which, genetically, were probably not identical with the races used by Straib. The statement that the germ tubes of the uredospores show a typical growth pattern depending upon the question of whether specific origins of wheat or barley were concerned, was given support by the fact that also biotypes from East Asia showed the same reaction.

In this situation the question is raised whether the division of the P. glumarum in formae speciales requested by Eriksson (1894) at the time is justified at least for the f. sp. tritici and the f. sp. hordei. In the taxonomical classification of the species into biological subdivisions, morphological and pathological considerations are determining in the case of parasitic fungi. With stripe rust the investigations on the reaction with regard to infection have caused Straib and other authors to deny the justification of formae speciales of Eriksson (for literature see Hassebrauk, 1962). Recently, Kajiwara (1964) vigorously advocated the retention of the old f. sp. tritici and hordei on account of the pronounced difference of pathogeny. Although the differences in the growth pattern of the uredospore germ tubes alone would hardly be sufficient to justify the status of the formae speciales, they can still be considered a point in favor of the suggestion made by Kajiwara. However, I do not consider it justified to substantiate a further subdivision. If a decisive significance would be attached to morphological or physiological peculiarities in connection with the germination, then this would violate the term of the "physiological" races and would represent a misunderstanding of the efforts made mainly in order to serve practical objectives to establish races as such (see Paragraph A. 2 and Paragraph B. 3.b)).

It is true Straib (1939a) had first held that the differences in the growth pattern of the germ tubes of individual stripe rust races which were distinguished from each other only indistinctly or not at all with regard to their pattern of affection, on the test assortment, would justify a subdivision into further races. Thus, he established race 46 which differed from race 45 only by another germ tube growth pattern; the situation is similar with regard to the races 47 and 28 isolated by him. Subsequently, Straib (1940) pointed out, however, that differences which appear exclusively with regard to the type of germination would not be suitable for a differentiation of races since the germ tube structures are connected with specific culture and germination conditions.

A special position is taken by the barley stripe rust races morphologically inasmuch as they form vesicles and secondary hyphae in vitro more readily than wheat rust races. The formation of these structures which had repeatedly given rise to speculation in the literature which was concerned with rust fungi is favored in the stripe rust among others by a high fructification and germination temperature. The result was a new cognizance: higher germination temperatures cause a formation of vesicles also in vivo on the surface of the leaf. Since the vesicles and the secondary hyphae emanating from them have a relatively long life compared to the normal germ tubes, it would be possible to interpret the vesicles as structures reminding us of "gems" or "emergency spores*" which could be significant epidemiologically inasmuch as they are able to keep the rust fungus alive for a long time when the process of infection is interrupted or delayed.

The vesicle formation found by me at higher temperatures in vivo may possibly be suitable for providing an explanation for the statement made by a few older authors who misunderstood these structures (for example, Eriksson and Henning, 1896) that the germ tubes of P. striiformis formed an appressorium during the penetration into the host plant. I never found a formation of an appressorium in agreement with Marryat (1907) and Allen (1928) in stripe rust races.

My investigations in connection with the germination physiology have shown that the doubts mentioned at the beginning with regard to the "moodiness" of stripe rust, as expressed by Wilhelm (1931), are justified. In the course of the investigations made on numerous races and origins, it has always been established again that the germination reaction of the stripe rust spores which often appears to be purposeless must be explained by a very sensitive reaction to the various environmental conditions. The environmental conditions induce a specific germination reaction in part as early as during the fructification time; however, they have a strong impact directly during the germination process proper.

My investigations have led to results which confirm, in principle, many of the regularities recognized for the first time by Straib and which have extended them in part. It was

*Emergency or secondary spores, distinguished from typical vesicles in various ways, were found by Gaertner and Fuchs (1962) under certain conditions of inhibited germination of black rust uredospores.

found that the temperature for the stripe rust represents a cardinal point in the meaning of Straib and others, but that the effect of temperature (and also of light) may be modified or superimposed by other factors. Thus, in terms of quality, germination substrates which seem to differ from each other only to a small extent may have a considerable impact on the germination behavior of stripe rust, as was observed by Manners (1950) and as have shown my tests conducted with various agar and gelatin origins.

In view of the different reaction of individual stripe rust races on certain environmental factors, it is not surprising that also the duration of the fructification time (also on host species sensitive to the same extent) varies. I have been able to establish this for the first time as a genotypically fixed property in individual races, which property is probably of significance in epidemiological respects, since races with a shorter fructification time have a higher maximum temperature and vice versa.

I recognized another two new factors which have a great impact on germination and, thus, also on the process of infection: the self-inhibition and the "weather factor." The self-inhibition of germinating uredospores has been established in numerous species of rust, but had not been established so far in P. striiformis. My investigations have resulted in a complicated pattern which, for the time being, must not yet be interpreted: no results were obtained with regard to the production of such inhibiting substances and the tolerance of the individual races to such inhibiting substances to permit a reliable insight into the development. The observation, according to which individual races of P. striiformis show a greatly diverging germination behavior in the presence of the same diffusate of the inhibiting substance which fluctuates between almost complete inhibition and almost unrestrained complete germination, must be emphasized since a similar difference in the behavior of the races had not been known up to the present in other species of rust.

So far the nature of the inhibiting agent has not been clarified; its analysis would require further investigations.

It is in the nature of the subject matter that the observations concerning the impact of the "weather factor" on the germination of uredospores remain unsatisfactory. On the basis of my observations there can be no doubt as to the presence of such an effect; my observations are also in agreement with the correlations repeatedly found by Bortels in other objects between certain developments of the weather and various biological reactions. However, the causality is still not clarified in all cases.

Still, the problem of the great germination fluctuations, which has hitherto been completely enigmatical, has now been defined more accurately by the establishment of a germination behavior in P. striiformis in reference to the weather.

On the basis of all these statements there cannot be any doubt that the germination and infection behavior of stripe rust is controlled by a number of factors to an extent not known with other species of grain rust. It would hardly be possible for an observer who is familiar with the subject matter to decide with certainty in each instance which factor determines the development of the germination to a greater or lesser extent. The extent of the response of stripe rust to one or the other factor was shown in the present investigations, particularly when comparative germination tests were conducted with P. recondita tritici. Reference to this has been made several times, for example, in the investigation on the impact of substrates on the germination *.

The partly unequivocal differences found in the behavior (reaction) of individual stripe rust races and particularly in certain biotypes, in terms of germination physiology, give rise to the question whether such differences should be used for stating and identifying a physiological race. In a certain physiological race we include all biotypes which provide an infection pattern on the recognized test species under the environmental conditions which have been recognized as being

*This statement was also made in another case which may be mentioned here: In an air-conditioned chamber, the walls of which had been provided with plates made of plastic material (Pegulan), agar plates seeded partly with stripe rust, partly with wheat brown rust uredospores, were prepared for germination in the dark in closed Petri dishes. At the same time controls of both spore origins were put under thermostatic check under the same temperatures. Whereas the brown rust spores had germinated evenly and almost completely after a certain time in the germination dishes of both places, this applied in the stripe rust spores of different races only to the thermostat; on the other hand, the germination dishes in the air-conditioned chamber showed only traces of germinated stripe rust spores. A change in the arrangement of the test made it possible to establish clearly that the inhibition of germination in stripe rust spores was caused by traces (!) of the solvent in the air of the chamber (a mixture of methanol, ethanol and toluol) which was contained in the putty used for the plastic lining.

optimal and can be easily reproduced, the patterns being in agreement with each other (see Hassebrauk, 1962, pages 13 and 185). Whereas a biotype is a biological individual, a physiological race represents a fictitious notion (compare also Stakman and Harrar, 1957, page 133). The determination of the physiological races serves mainly to cultivate resistance; therefore, the ascertainment of its pathogeny must be given preference. If a biotype stands out on account of its characteristic pathogeny for additional test varieties or by a deviating infection behavior during changes of environmental conditions, particularly of temperatures, from the group of biotypes which are grouped in a physiological race, it has become customary to add a suffix to the race number. Practical requirements would not be met if new races would only be stated on the basis of special needs, in terms of germination physiology, of some biotypes. Straib (1941) called a biotype from the Tyrol, of race 6, which stood out by other cardinal points of the germination temperature, only as a race 6x in subsequent analyses of stripe rust races. We must support Straib when he states at another place (1940, page 234) that the investigations in the field of germination physiology and the determinations of the pathogeny supplement each other, but that they cannot replace each other.

In conclusion a brief reference may be made to a repeatedly discussed point which is raised on account of the results of my investigations: to what extent can a relationship between the geographical distribution of the epidemiology of races and their germination properties be established? We can count on such relationship only under certain conditions, if at all. Among the races which I tested, race 26 from Holland, for example, showed the highest maximum temperature. Within the European biotypes (Switzerland, France), great differences in the temperature needs of one and the same race were established; this statement was made by Straib (for example, 1939a; 1941) several times in a similar form. If, in some cases, certain factors appear to support such relationships, in any case as far as the temperature is concerned (higher germination rate and higher maximum temperature of the Greek and Turkish biotypes as against the German one in race 20 A), then such phenomena must not be overestimated. In this regard I consider more reservation appropriate than was shown by some of the former authors. So many factors are involved in the geographical distribution of the races and the epidemiology that too much emphasis on one factor or on a few factors must lead to erroneous conclusions. The main point is the primordial significance of the sensitivity of the species which is again highly variable depending upon the environmental conditions, and of the distribution of species (Gassner and Straib, 1934). Further factors enter the picture in connection with stripe

rust which can be of subordinate significance with other species of rust. This was evidenced by the present investigations and, in several instances, newly recognized factors were added to those which have been known in the past.

The above work was begun in April 1961 and completed at the Institute for Botany of the Federal Biological Institution, Braunschweig.

I am very grateful to my honored teacher, Prof. Dr. K. Hasselbrauk, for suggesting this theme, rendering advice, and all-round encouragement.

To the President of the Federal Biological Institution for Agriculture and Forestry, Prof. Dr. Dr. h. c. H. Richter, I am indebted for having provided me with a position.

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*The article was available only through a report (Biol. Abs., Vol 41, No 4, 16437 (1963)).

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"Cross Protection with Two Rust Fungi," Phytopathology, Vol 46, pp 540-544.

RESUMÉ

I, Juergen Schroeder, was born on 10 September 1930, the son of Werner Schroeder, at the time high school teacher with permanent employment status, and his wife Franziska née Leue, at Braunschweig.

After having attended the elementary school from 1937 until 1941 and, subsequently, the Gauss School (municipal high school with natural sciences and modern languages) at Braunschweig, I took the graduation examination there in February.

Subsequently, I studied two semesters of biology each starting in the summer semester 1950, first at the Technical Academy of Braunschweig and then at the University of Freiburg i. Br. From the summer semester 1952 through the summer semester 1955 I continued my study of biology with chemistry as a minor at the University of Marburg-on-Lahn.

In January 1956 I started practical work at the Hagenmarkt Pharmacy at Braunschweig and took the Preliminary Pharmaceutical Examination at Braunschweig in March 1958 after two years of practical work at the pharmacy.

Subsequently, I studied pharmaceutics at the Technical Academy at Braunschweig and passed the Pharmaceutical Examination here on 22 April 1960.

From May until September 1960 I worked as a candidate of pharmacy at the Linde Pharmacy at Goettingen-Weende, and, subsequently, I married in September 1960.

In November 1960 I obtained a position with the Federal Biological Institute of Braunschweig-Gliesmarode. Since that time I have been working there on my dissertation in the field of phytopathology with Professor Dr. K. Hassebrauk.

From February 1961 up to the present time I also was an assistant at the Hagenmarkt Pharmacy (Braunschweig) on a free-lance basis; in September 1961 I was given the approbation as a pharmacist.

THE END